The Planning And Control Of Action In Normal Infants And Children With Williams Syndrome.

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Abstract

The development of action control was studied in normal infants between 5-15 months and in children with Williams syndrome, a group in whom it is thought that the visual processing stream controlling action (the dorsal stream) may be specifically impaired. In the first set of experiments, looking and reaching measures were taken as infants were resented with pairs of objects of different sizes. An increase in frequency of reaches to raspable objects and in the time spent inspecting objects before reaching was observed after 8½ months, reflecting a developing ability to use visual information to predict the 'graspability' of objects. There were concurrent changes in the kinematics of the reach; infants at this age exhibited slower reaches, with an extended 'homing-in' phase. referential looking measures showed that as infants get older, visual orienting to objects in personal space becomes less dependent on the visual salience of the object. Lastly, there was evidence that reaches tended to follow the direction of the first look in any given trial. Flexibility in the choice of a target for reaching may therefore depend upon the development of an ability to selectively inhibit neural circuits controlling looking and reaching.

The second set of experiments investigated how far the visuo-motor difficulties experienced by children with Williams syndrome are due to atypical dorsal stream development, or in the ability to plan ahead in simple actions. The ability to adapt grip size to object size (a 'dorsal stream') function was compared with the ability to make a perceptual size judgment (a 'ventral stream' function). Deficits were observed in both tasks, with no relative deficit in dorsal stream, compared to ventral stream function. Tests of motor planning indicated that children with WS are less likely than controls to select an initial grip that ensures a comfortable end-state posture of the arm. However, this ability seems to be unevenly distributed in children with WS. Further work will need to be done to identify whether these differences between individuals are related to different compensatory strategies or are correlated with the extent of the genetic deletion in WS.

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Part of the research presented in chapter 1 is in press (Developmental Psychology).

The data presented here is archived with the Visual Development Unit, Department of Psychology, University College London, Gower St. London WC1.

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PAGINATION AS IN ORIGINAL

1 Introduction

In order to visually select and then reach out to grasp an object, infants need to transform visual information about the location, size, shape, orientation and estimated weight of objects into an accurate and coordinated set of motor commands. They must at first attempt this using a motor system which is not yet fully myelinated (Armand *et al.* 1996) and whose output may be unpredictable (Berthier, 1994). In addition, prehension involves the co-ordination of functionally separate components (the hand and the arm), the control of which may be developing at different rates (Jeannerod, 1988). Furthermore, if they are to avoid reaching for inappropriate objects or surfaces, they must appreciate the relationship between the size of an object and the size of their hand. A further level of processing is introduced when children start to adapt their actions according to the intended use of the object. So, for instance, a different grip might be chosen depending on whether a child wishes to pass a crayon to a friend or to draw with it.

This thesis reports on a series of studies designed to investigate the normal and atypical development of this ability to plan and control action. These studies have concentrated upon the reach-to-grasp movement because of its early age of onset; infants start to reach and grasp objects at around 4 months. In addition, as this movement has been extensively studied in adults, its typical characteristics are known and so there is a clear end-point with which developmental data can be compared. There are also coherent models available of the control processes underlying prehension, which have been mapped onto what is known about the underlying neurophysiology with a fair amount of success.

As will become apparent in the following chapter, a number of neural subsystems are potentially involved in controlling eye and arm movements in adults (Atkinson, 2000). Relatively little research has been done into how these systems interact in determining motor output in infants, nor is very much known about how far these systems are functionally or neurally differentiated in early infancy. The infant studies reported here attempt to answer these questions by observing both looking and reaching behaviour whilst infants select and reach for objects of different sizes and visual pattern.

The second part of the thesis extends the study of action control development to an atypical population, children with a genetic disorder known as Williams syndrome (WS). Because of the uneven cognitive profile associated with WS, it has often been claimed that this syndrome provides an example of genetically determined impairments in neural, and consequently cognitive, development. For example, it has been proposed that the visuospatial and visuomotor impairments associated with WS result from an impairment in the dorsal relative to the ventral stream of visual processing. Thus by studying how children with WS use visual information to control their actions, we may learn how visuomotor abilities develop in a population in which the brain structures normally critical to these abilities may be specifically impaired.

This chapter will serve as an introduction to both lines of study, by reviewing what is known about the control of visually guided action, at functional and neurophysiological levels, as well as describing developmental studies. Some discussion will also be necessary of the selection processes that precede action. Literature specific to Williams syndrome will be reviewed at the beginning of chapter 5.

1.1 THE CO-ORDINATION OF PREHENSION IN ADULTS.

All skilled actions involve the co-ordination of several separate components, as different muscle groups must act in concert to effect any action. When reaching out and grasping an object, the components that must be coordinated are the movement of the arm that brings the hand to the required location, and the adaptation of the grip to the size, shape and use of the object to be grasped. Observation of reaching and grasping movements shows that hand shaping occurs during reaching, and that it anticipates the properties of the target object. The two components must also be accurately coordinated in time - the finger grip must close at the right moment as the hand approaches the target.

When the kinematics of the mature reach and grasp movement are studied, a number of typical features can be observed (Jeannerod, 1984; also see Figure 1.1). The velocity profile of the reach has a single peak, with a bell shaped profile. The fingers open to a maximum aperture which is strongly correlated with the size of the object being picked up. The time at which the fingers open widest corresponds with a discontinuity in the deceleration phase of the reach (a point where 'velocity became constant or started to increase again before the movement stopped'). This velocity change is thought to coincide with a reparametrisation from a body-related to an object-related frame of reference (Jeannerod, 1988). The proportion of total time taken up by each phase is relatively constant, with the transport phase taking 70-80% of total movement time.

1.1.1 The visuomotor channels hypothesis

The two components of prehension are not only separable in terms of the muscular movements involved but also in the type of information required before each

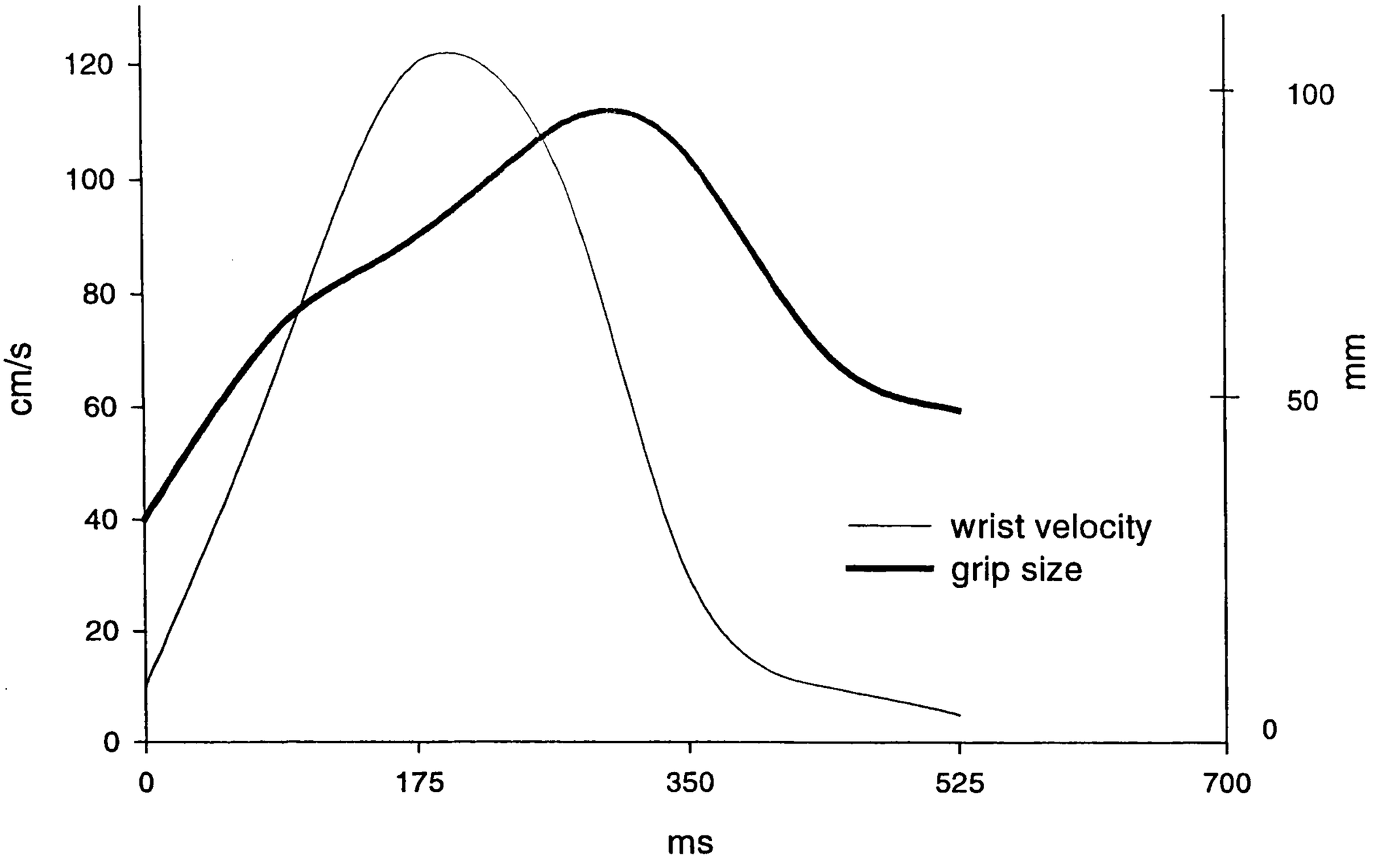


Figure 1.1 Kinematics of normal prehension.
Graph adapted from Paulignan and Jeannerod, 1996

of the two components can be initiated. Hand transport is concerned with extrinsic properties of the object - its orientation, height and distance from the body, whereas hand aperture is concerned with intrinsic properties such as its size, mass, shape, texture or estimated centre of gravity.

Jeannerod (1984) has proposed that in the case of prehension, separate mechanisms or 'visuomotor channels' exist to deal with extrinsic and intrinsic properties of the object, and thus that hand transport and hand aperture are therefore controlled by separate channels. In Jeannerod's view, the visuomotor channels are specialised input - output structures, which 'generate appropriate motor responses, in different sets of muscles, from the limited number of parameters that are extracted by their respective visual inputs'. Information about an object's location will be processed in the reach channel, whereas information about its size will be processed in the grasp channel. There is no need, in Jeannerod's view, for these attributes to be 'bound' into a single object percept for a successful action towards the object to be carried out.

The separate channels are seen as only being loosely co-ordinated in terms of starting and ending at the same time, but not sharing information during the action. Jeannerod provides a description of the temporal co-ordination of the two components during reaching and grasping and also provides evidence for separate control mechanisms. In his first experiment Jeannerod filmed subjects reaching and grasping a variety of objects. In some trials subjects were prevented from gaining visual feedback whilst making the movement - through a system of mirrors they could see an image of the object which corresponded in position with the actual object, but could not see their own hands as they reached for the object. This was not found to significantly alter duration or maximum velocity of the action - only affecting accuracy in that there was a frequent, small undershoot in grasping, though the grip was perfectly formed for the

object in question. This corresponds with Keele's (1968) conception of a motor program, as 'a set of motor commands that are structured before the movement begins, that allow the sequence to be performed without any peripheral feedback'. Jeannerod suggests that the two components share only a common 'go' signal and are then informationally distinct; the very last portion of the movement may be under the control of visual feedback in order to ensure final accuracy.

The two components were found to be linked in the sense of 'covariation of the time axis', for instance the time of maximum finger grip aperture and the time where transportation movement reaches maximum deceleration was exactly the same in 68% of the trials, and varied by no more than 80 ms in the rest of the trials. Thus a limited number of critical points on the time axis - simultaneous release and the point of convergence of velocity curves - are defined by the motor program. Jeannerod suggests that it is this point of convergence that is the goal state of the motor program, rather than actual contact with the target. This allows time for final homing in on fragile or small objects.

In order to investigate whether the two components of prehension were independent, a second experiment was then carried out in which the shape of the object was unexpectedly switched at the onset of movement (an elliptical object that, when presented 'head on', appeared to be a sphere was rapidly rotated, giving the subjective experience of an instantaneous change of shape). No change was observed in the transportation component of the action, even though the grip component had to be modified in mid-action. Thus, motor commands controlling prehension can be selectively modified during movement. However, this sudden increase in load on the system only affects the relevant channel, supporting the view that the channels are not sharing information during movement.

There is also developmental and physiological evidence for separate components. In infants (monkeys and humans) the ability to reach for an object develops before the ability to grasp objects successfully (Kuypers, 1962; Hofsten,1989) In monkeys the difference in development times for transport and grasp components of prehension is thought to reflect differential rates of maturation of cortical and motorneuronal synapses that control independent hand and finger movements (Kuypers, 1962, cited in Jeannerod,1994). Also evidence from localised brain lesions in monkeys shows that damage to the pyramidal tract - the set of descending neurones running from the cerebral cortex down into the spinal cord - can cause impairment of fine finger movements without affecting the ability to transport the hand near to the object (Lawrence and Kuypers,1968).

Besides behavioural evidence that reaching and grasping depend to some extent upon different descending pathways, there is also neuropsychological and neurophysiological evidence that the visuomotor transformations underlying the two components of prehension are anatomically separable. The following section will describe the neuronal pathways underlying the control of manual action.

1.2 NEURONAL PATHWAYS UNDERLYING REACHING AND GRASPING.

A large body of research evidence now shows that a set of interconnected areas in the posterior parietal region and pre-motor cortex are crucial to the neural processing underlying reaching movements. The posterior parietal cortex (PPC) lies between the visual areas of the brain and the prefrontal areas which control movement. This area of the brain is thought to be involved in the transformation of information of visual information about target and limb position into appropriate motor acts. (Areas of the

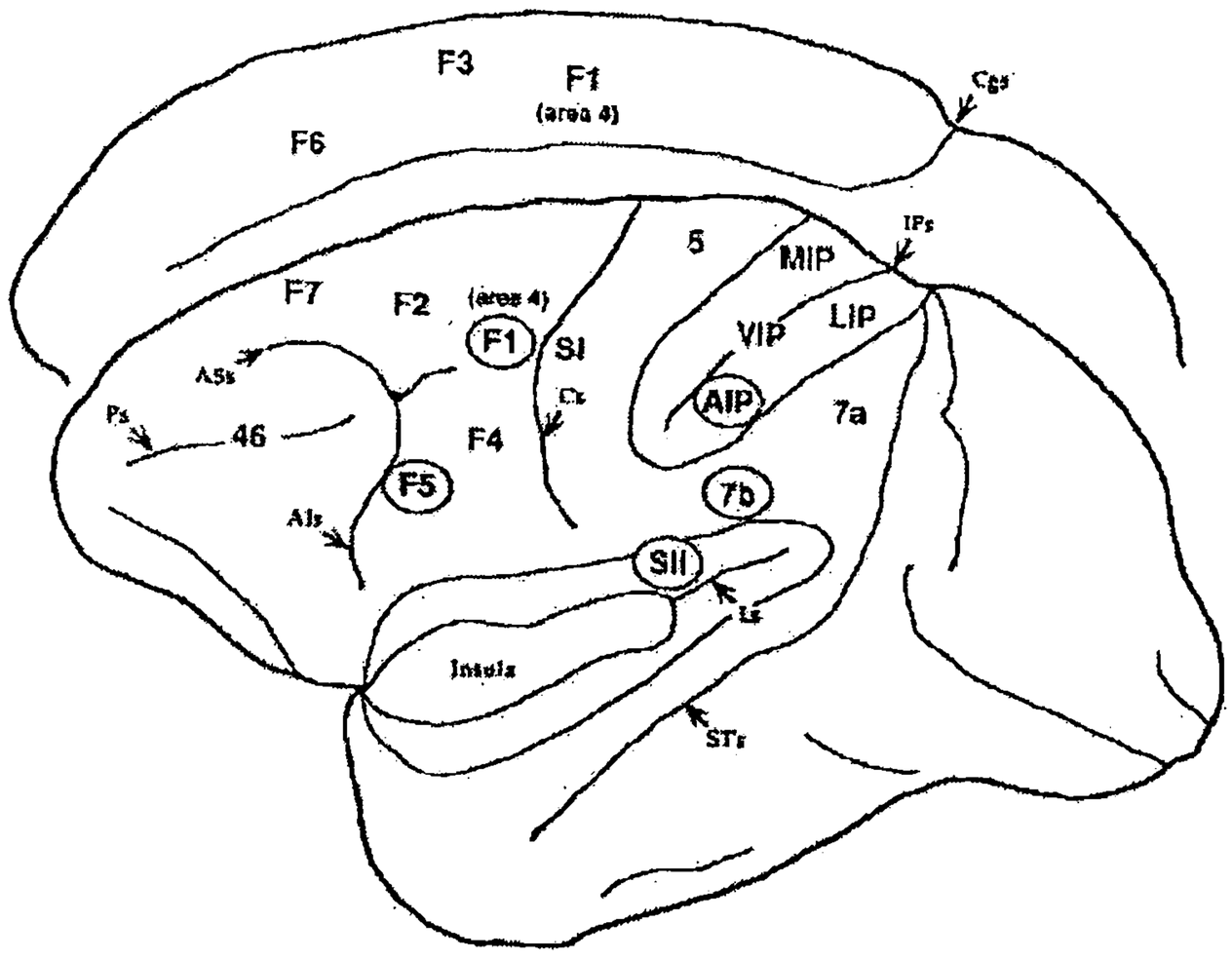


Figure 1.2 Areas of the macaque monkey cortex involved in the control of prehension.

Abbreviations: AIP – anterior intraparietal area. IPS - intraparietal sulcus. LIP – lateral intraparietal area. FI – primary motor cortex, MI, area 4. MIP – medial intraparietal area. F4, F5 – parts of ventral premotor cortex involved in arm (F4) and hand (F5) movements. 7a, 7b – fixation and reaching areas of the inferior parietal lobule. F3, supplementary motor area. F6 – pre-SMA. SI – somatosensory cortex. SII –second somatosensory area.

macaque monkey cortex involved in the control of prehension are shown in figure 1.2.).

The PPC is divided into superior and inferior regions by the intraparietal sulcus. Neurons related to visually guided reaching and manipulation have been identified in areas 5 and 7 and were from the start classified *as reach-related* and *manipulation-related* neurons (Mountcastle,1975; Hyvarinen and Poranen, 1974). In the monkey, area 5 is the caudal part of superior parietal lobule (SPL), while areas 7a and 7b form the inferior parietal lobule, (IPL) (Rothwell, 1994). In addition, discrete areas of pre-motor cortex have been identified which are related to reaching and grasping. (Rizzolati, 1997)

1.2.1. Reach related neurons

A number of versions of possible 'reaching circuits' have been described that involve connections between posterior parietal cortex and pre-motor cortex. One such parietal-to-frontal circuit involves connections between the areas 7b, which is linked with arm movements, and inferior pre-motor cortex, specifically area F4 (Matelli *et al.* 1986) Inferior pre-motor cortex is somatopically organised, with neurons representing arm movements situated in the F4 subdivision (Matelli, 1986), whereas neurons related to hand movements are situated mainly in area F5. Cells in F4 code the location of a visual stimulus according to its location in the space around the body, independent of eye position. This kind of coding of target position is necessary for the visual guidance of movement (Gentilucci *et al.* 1988). Milner and Goodale also describe a parieto-frontal pathway involving ventral intraparietal cortex (VIP) and F4.

Other workers, oppose the idea that the visual transformations underlying reaching take place in a serial fashion in clearly defined circuits. Instead they cite evidence for overlapping populations of cells in both PPC and frontal motor areas, which seem to form visuospatial-to-motor processing 'gradients' (see Kalaska *et al.* 1997; Caminiti *et al.* 1998, for reviews).

It should also be noted that interruption of the pathways between the visual areas and motor cortex does not completely eliminate the ability to carry out skilled reaching movements in monkeys. Glickstein (1998) describes a alternative pathway connecting parietal lobe to frontal motor areas, which passes via the pontine nuclei and the cerebellum. The cerebellum is thought to use efferent copy of the motor command to predict the current position of the limb, thereby avoiding feedback delays in the online control of movement (Miall, 1998). This area is also thought to be crucially involved in motor learning, (for a review of cerebellar structure and function, see Stein and Glickstein(1992)).

1.2.2. Manipulation related neurons

Manipulation related neurons are concentrated in the anterior intraparietal area (AIP), a small zone located within the intraparietal sulcus (rostral part of posterior bank). Taira *et al.* (1990) identified neurons in this area which were selectively activated during particular grip configurations, independently of the position of the hand in space. Thus, these neurons were related to hand and finger movements, not arm movements (Jeannerod, 1996). Taira *et al.* (1990; see also Sakata, 1997) replicated this result, and went on to investigate the contribution of visual signals to the activity of these neurons, by measuring their activity during grasping movements made both in the light and in the dark. The neurons were grouped into three types:

Motor dominant neurons showed the same level of activity whether the movement was performed in the light or in the dark.

Visual-and-motor neurons showed less activity during manipulation in the dark.

Visual dominant neurons were not active during manipulation in the dark.

Other neurons in this area seemed to be related to the sight of the hand rather than object fixation. The activity of many of the visually responsive neurons was object-specific, in that they were more active during manipulation or fixation of the same object. (see Fig. 4, Sakata, 1997 which shows a neuron which is significantly more active during manipulation and fixation of a square plate, but not during manipulation or fixation of 5 other objects, ring, cube cylinder, cone or sphere.) Other neurons, which were not so specific in their activity, nevertheless showed a preference for a certain class of three-dimensional shapes. For instance, some visual dominant neurons were more active during fixation of the round shaped objects (sphere, cone, cylinder) whereas others preferred the angular shapes (cube, square plate).

So, cells in area AIP seem to be tuned for the three-dimensional features of objects, when they are about to be, or are being manipulated. Sakata proposes that AIP receives signals about 3-d shape from cells in caudal intraparietal sulcus (cIPS). He has identified two kinds of neurons in this area: Some cells showed preference for a particular object orientation, regardless of stimulus thickness or length. Others were sensitive to the orientation of a flat surface, regardless of its shape. These cells may represent an intermediate stage of processing between visual areas and area AIP (Rizzolati at al 1997)

The importance of area AIP for the manipulation of objects has been confirmed in a study carried out by Gallese *et al.* (1994). Injection of area AIP with the GABA agonist muscimol, caused errors in the pre-shaping of the hand during a precision grip. By contrast, injection of a more caudal area of the intra-parietal sulcus caused misreaching. Confirmation that AIP deals with visuomotor aspects of grasping is given by the observation that the monkey was able to grasp the object correctly once it had touched it. This study also provides neurophysiological support for Jeannerod's visuomotor channels hypothesis.

Area AIP is directly connected with area F5 (the post-arcuate region of ventral pre-motor cortex). This area also contains neurons which are related to object related actions. Rizzolati *et al.* (1988) report that most neurons in F5 in the monkey are related to grasping, tearing, holding or manipulating objects. 85% of these neurons are selective for a particular kind of grip (precision, finger prehension, or whole hand prehension). This would seem to be similar to the activity of neurons in AIP, some of which are also selectively activated during certain grip formations. Indeed, the effects of reversible inactivation of both areas is very similar – a deficit in grasp formation but no disruption of reaching. (Gallese *et al.* 1997).

However there are important differences (Jeannerod, 1996). The timing of neuronal discharge is different in the two areas. AIP neurons start to fire during pre-shaping of the hand, and continue whilst the monkey is holding the object. In F5, on the other hand, different cells fire selectively during different stages of the grasp. Jeannerod proposes that whilst AIP neurons represent a complete grasping action, F5 cells code for particular segments of the grasp. Rizzolati (1997, 2000) has a slightly different interpretation. He suggests that AIP provides a selection of object descriptions to area F5. Neurons in F5 then select the most appropriate grip, according to context, and also code for specific phases of the grasp, such as aperture and closure.

Rizzolati *et al.* also report on another class of cells in F5, which may have particular relevance for the representation of motor acts. These 'mirror neurons' respond both during the performance of a particular hand movement, and during observation of the *same* movement. Other neurons seem to encode the aim of a motor act, regardless of the effector used to achieve it – neurons which respond when an object is grasped in the hand, *or* in the mouth. Rizzolati believes that pre-motor cortex contains a vocabulary of motor acts, such as reaching, grasping or holding (Rizzolati, 1987). The firing of the mirror neurons may underlie abstract representations such as the recognition of motor events. (Rizzolati *et al.* 1996). He also argues for a similar observation/execution matching system in man, based on TMS and PET data (see below). F5 is itself connected to an area of primary motor cortex (MI) related to hand movements (Jeannerod, 1996). MI is the area of the brain from which most motor commands are issued, the beginning of what Sherrington (1947) called the '*final common path*'' to the muscles. Neurons in MI are even more specific in the segments of a movement that they code for, with many standing in a one-to-one relation with particular muscles.

1.3 HUMAN VISUOMOTOR PATHWAYS: EVIDENCE FROM PET/FMRI

1.3.1. Areas activated whilst reaching, pointing and grasping

A number of studies have used PET to identify areas of the brain activated during prehension (see Table 1). Grafton *et al.* (1996) have studied the brain areas involved in reaching and grasping, using positron emission tomography. Regional cerebral blood flow (rCBF) was measured whilst subjects reached out and grasped simple cylindrical objects, and also whilst they were pointing at the same objects. A control condition was included in which subjects simply looked at the objects. Activity was increased during both reaching and pointing in primary motor cortex, premotor cortex and ventral supplementary areas contralateral to the reaching hand. The motor area of cingulate cortex, the superior parietal cortex and dorsal occipital cortex were also activated. Interestingly, from the point of view of a comparison with electrophysiological data from the monkey, there was a relative lack of activation in the intraparietal fissure. (Recall that areas VIP and AIP were associated with reaching and grasping movements in the monkey brain). Parietal activation was rather in the superior parietal lobe, which in humans contains Brodmann's areas 5 and 7 (in the monkey area 7 is inferior to the IPS). Superior parietal cortex has been associated with tasks requiring visuomotor transformation in a number of PET studies (Roland *et al.* 1980). Also there was no activity in ventral pre-motor cortex, which in the monkey contains areas F4 and F5, areas implicated in the control of prehension and possibly the recognition of motor acts (see above). The only area in which blood flow was significantly increased during grasping an object compared to simply pointing towards it, was the left parietal operculum (secondary somatosensory cortex, BA 2,40.). Grafton *et al.* speculate that this area may be involved in the processing of object shape based

upon tactile information, as focal lesions of the parietal operculum cause tactile agnosia with no loss of sensation or motor control.

1.3.2. PET studies of observed and imagined actions

Rizzolati *et al.* (1996) have extended this investigation to include observation and imagination of grasping actions. The aim of these experiments was to see whether PET would reveal areas specific to the observation of hand actions in man, similar to those found in the monkey (see section 1.2.2).

In this study, the reaching movements were compared with observation of the experimenter doing the same movement, with simple observation of the objects as a control condition. In this study, a number of cortical sites were more activated during reaching than object observation. These were motor and somatosensory areas 1,2 3,4, the left superior parietal lobe , the cuneus, the left putamen and both hemispheres of the cerebellum. Again, there was no activation in areas corresponding to F5. Grasp observation activated regions in the left inferotemporal lobe (area 21) and the left inferior frontal gyrus (inferior area 6 and areas 44 and 45). This area corresponds to the rostral part of Broca's area. Why was there no common area of activation for observation and performance of grasping actions, as the monkey evidence would predict? It may be that such an area does not exist. Alternatively, the task demands of these experiments may be different. There is some evidence from PET for a hand representation in Broca's area (see p 250, Rizzolati *et al.* 1996). Whilst their own evidence does not support such a view, they wish to argue that cells which encode both action and observation of action may be located in Broca's area. This permits a further speculation; that the origin of language may lie in the observation of meaningful actions.

Table 1.1 Areas preferentially activated in PET studies investigating brain areas involved in object oriented action and object identification.

Data drawn from Grafton et al. (1996), Faillenot et al(1997), Rizzolati et al. (1997), Haxby et al. (1994). (Figures in brackets are Brodmann's areas)

Task studied	**Brain areas activated**
Reaching	Superior parietal lobe (5,7) Motor cortex (4) Premotor cortex (4) Somatosensory areas (1,2,3.)
Grasping vs pointing	Parietal operculum (SII, areas 2/40)
Grasp Observation	Left inferotemporal cortex (21) Left inferior frontal gyrus (inferior area 6, areas 44, 45)
Face matching	Ventral occipitotemporal cortex (17,18,19)
Location matching	Inferior parietal lobe (7) Dorsal occipital cortex (19)

1.3.3 A model of the control processes underlying prehension

The processes underlying prehension have been modelled by Arbib (1985, see Figure 1.3.) This model consists of a hierarchically organised set of 'motor schemas'. A motor schema, according to Arbib, is a set of motor commands which can act as a unit when programming an action. Motor schemas are activated by perceptual schemas – a specific subset of the visual information from the environment which specifies action-relevant properties of objects. These schemas can theoretically be recursively

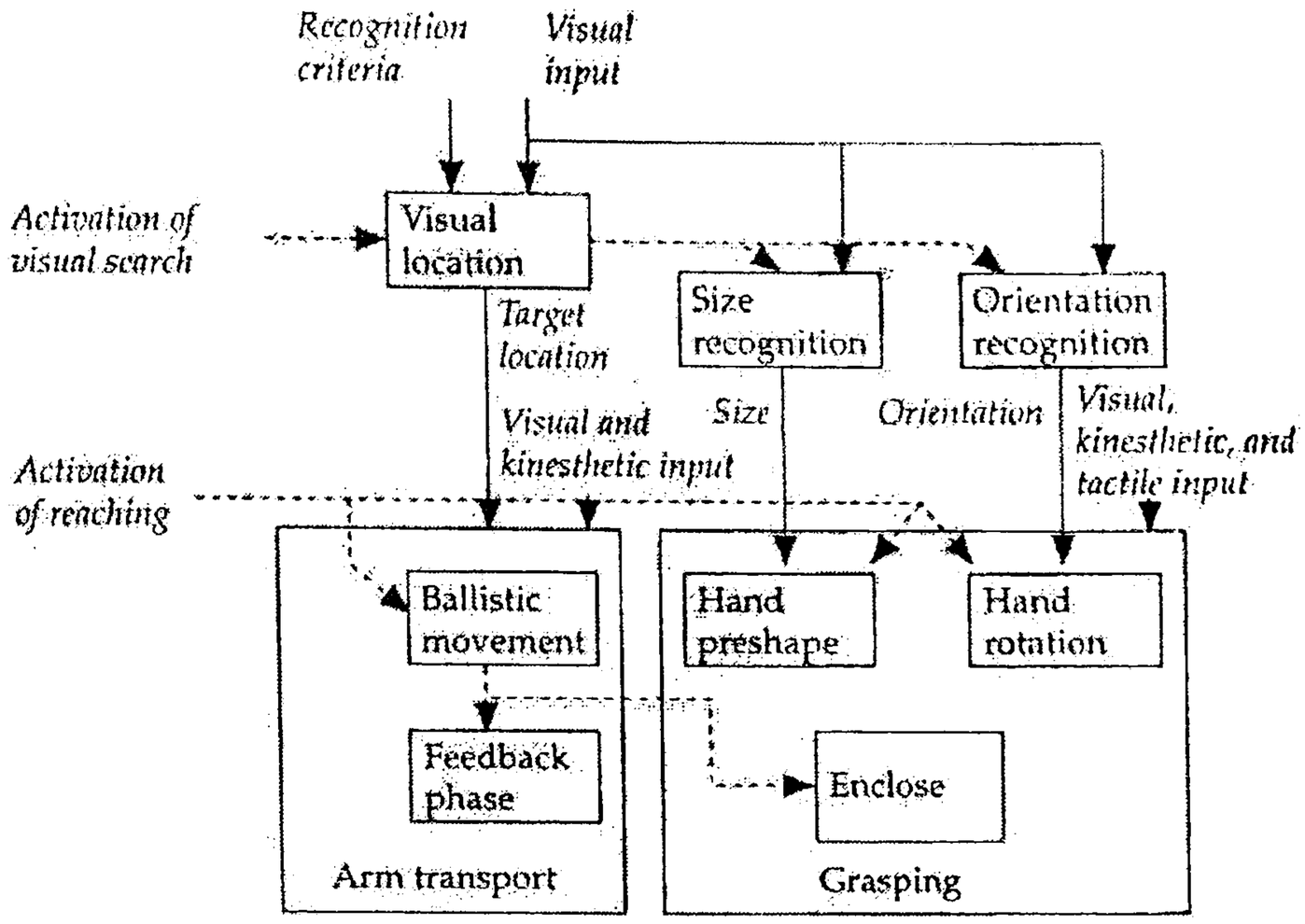


Figure 1.3. Model of the control processes underlying prehension (from Arbib,1981)

organised, so, for example, a schema for a pincer grip could be contained within a larger reach and grasp schema, which could be recruited within a higher level schema for sorting mail into mailboxes. Arbib and others (see Jeannerod, 1996; Fagg and Arbib, 1998) have attempted to map this model onto what is known about the response properties of neurons in the visuomotor areas of the brain described above. However, in order to discuss such models, we will need to set the reach and grasp pathways described above into the context of other brain areas that perform object related visual processing. (The Fagg and Arbib model of the functional neuroanatomy of prehension is shown in Figure 1.4.)

1.4 SEPARATE VISUAL PATHWAYS FOR PERCEPTION AND ACTION?

As can be seen from Figure 1.4, the neural pathways underlying prehension can be functionally grouped within a broader division of visual processing in the cortex. Visual input from the retina is passed to the cortex along a number of separate pathways. In the macaque, two diverging pathways from primary visual cortex have been mapped in the visual system. The ventral stream, passes to infero-temporal cortex, the dorsal stream passes to posterior parietal cortex (PPC). Ungerleider and Mishkin (1982) proposed that different kinds of visual information are processed in the two streams. Visual recognition is thought to take place in the ventral stream, whereas the dorsal stream is responsible for the localisation of objects. This proposal is based on the finding that monkeys with lesions of the inferotemporal or posterior parietal cortex show different patterns of impairment. Monkeys with IT lesions were impaired in discrimination of visual patterns. Monkeys with PPC were less successful in using spatial cues to locate items of food. So the key distinction in this account is between different visual attributes of an object - *what* and object is and *where* it is. These two streams of information are seen as contributing to a unified representation of the world, which is then available to both the cognitive system and action systems.

Milner and Goodale (1995) have proposed an alternative functional significance for the 'two visual systems'. They claim that the essential distinction between the ventral and dorsal streams is that they transform visual information for different purposes. Their argument is that visual systems delivering representations which can serve as the basis for further cognitive operations may be more recent, in evolutionary terms, than systems which directly control action. The dorsal stream, they propose, is

involved in the 'online' control of skilled action, whereas the ventral stream is involved in construction of the viewpoint-independent representations of objects which underlie cognitive operations and conscious perceptual experience. They cite a range of neuropsychological and neurophysiological evidence in support of this claim.

1.4.1. Neuropsychological evidence

Optic ataxia. Optic ataxia is an impairment in reaching observed after damage to the PPC. Patients are unable to reach accurately to objects in the visual field contralateral to the lesion. In Ungerleider and Mishkin's account, PPC damage should cause an impairment in the 'where' channel; the ability to accurately locate objects is lost. Damage to the PPC, therefore, should not affect processing of the properties of objects, as this should be dealt with in the 'what' channel. However patients with optic ataxia have problems not just with accuracy of reaching but also in forming an appropriate grip and hand orientation for a given object. Despite this impairment they can still correctly describe the orientation of an object (Perenin and Vighettto, 1988). (Also see Jakobsen *et al.* 1991, whose patient could recognise drawings of objects, but could not accurately adjust grasp size when attempting to pick up the same objects).

Visual agnosia. If the key distinction between ventral and dorsal stream processing is between object recognition and object location, damage to the IT cortex should leave all object-based information unavailable for any purpose, whether it be recognition or action. However patient DF, with visual form agnosia, is unable to perceive size, shape or orientation of objects. Nevertheless, she can reach out and grasp the same objects quite accurately (Milner *et al.* 1991).

Further support for the division of visual function proposed by Milner and Goodale was provided by Goodale *et al.* (1996), who compared performance in patients

with ventral and dorsal stream damage in a task which tests the ability to identify the centre of mass of an object from visual cues. In this experiment two patients were compared in their ability to use visual information to select an appropriate grip configuration for objects of different sizes. One patient (RV), had a bilateral lesion of the occipitoparietal cortex, resulting in optic ataxia. The other patient (DF), who has been discussed previously, developed visual form agnosia after suffering carbon monoxide poisoning. This patient is unable to discriminate between objects on the basis size or orientation, yet is able to accurately reach out and grasp the same objects.

The two patients and a single control subject were asked to pick up a selection of irregularly shaped objects using a precision grip. The points on the object boundary at which the thumb and index finger first contacted the objects were recorded and the centres of these points used to calculate 'grasp lines' passing through the object. At the same time, the patients were tested on their ability to visually discriminate between the objects. There was a clear dissociation between the patterns of impairment in the two patients. Whilst the control subject, and patient DF placed their fingers at points such that the grasp lines tended to pass through the centre of mass of the object, this was not the case for RV. (Interestingly, RV did correct the position of the fingers *after* initial contact, indicating that that she was still able to use tactile information to control grasp placement). On the discrimination task, DF was unable to tell whether pairs of the objects were the same or different, whereas RV and the control subject had no difficulty with this task.

Patient DF was also unable to match the orientation of a hand-held card with a slot that could be rotated to a range of angles (a perceptual matching or ventral stream task). However, when she was asked to actually 'post' the card through the slot (an

action control or dorsal stream task), her performance was as good as that of normal subjects (Goodale *et al.* 1991)

1.4.2 Neurophysiological evidence.

Milner and Goodale cite the neurophysiological evidence that there are networks of cells in the parietal and frontal lobes of the monkey cortex that seem to be involved in the transformation of visual information from retinal to body-centred reference frames as well as in the control of arm movements (see above, section 4.2). In particular, the presence in area AIP of cells that fire preferentially when the same object is fixated or manipulated (the visual-and-motor neurons described in Sakata *et al.* 1997; see section 1.2.2), seems to indicate that PPC is involved in the coding of the intrinsic features of objects. This would not be predicted under the 'what/where' distinction proposed by Ungerleider and Mishkin, but is consistent with Milner and Goodale's view that the critical aspect of the dorsal stream is its transformation of visual information for the control of action.

1.4.3. The ventral dorsal distinction – evidence from brain imaging studies

PET has been used to try to resolve the question of whether the ventral dorsal distinction is primarily a "what and where" distinction or whether the dorsal stream is primarily concerned with visuomotor tasks. Some studies have shown differential activation in dorsal and ventral stream areas during location and identification tasks. However, there is also clear evidence from PET that dorsal stream areas in humans are involved in reaching and grasping (see above, and Table 1).

Haxby *et al.* (1994) used PET to demonstrate a double dissociation between cortical areas involved in face matching and location matching. Regional cerebral blood flow was greater in both matching tasks than in a control task in which the subjects had to make the same motor act (a button press) and saw the same

configuration of stimuli. Both matching tasks gave rise to increased activity in primary visual cortex and posterior extrastriate cortex. However, in the face matching task, increased activity was also observed in ventral occipitotemporal cortex (BA 17,18,19), whereas location matching resulted in increased activation in dorsal occipital cortex (BA 19)and the inferior parietal lobule (BA 7). An area that contributes to both tasks was observed in dorsal occipitoparietal cortex.

Faillenot *et al.* (1997) have compared rCBF in subjects performing shape matching or grasping tasks. A pointing task was used to subtract out the motor aspects of the grasping task. Dorsal stream areas contralateral to the reaching hand were preferentially activated during the grasping task, whereas right ventral stream areas were activated during the matching task. When grasping was compared with pointing, an area of parieto- insular cortex (BA 2, 40) was activated (closely corresponding to that observed in the similar condition of the Grafton *et al.* (1996) experiment, which they refer to as the parietal operculum). One area was found to be activated in both tasks, the junction of Brodmann areas 7 and 19 (this area was found to be activated in both location matching and location working memory tasks in Haxby *et al.* 1994 and Courtney *et al.* 1996). As discussed above, this evidence of dorsal stream involvement in shape recognition speaks against a strict segregation of function between the two streams. Further evidence that the distinction between processing streams may not be anatomically clear-cut has been provided by Braddick *et al.* (2000), using a pair of tasks designed to compare dorsal stream function with ventral stream function, the *motion and form coherence* tasks. The *motion coherence* task tests the ability to perceive a strip of dots which move as a group, amongst other dots which move in random directions. By varying the ratio of coherently moving dots to randomly moving dots (the signal to noise ratio) a motion coherence threshold can be determined, which serves as a measure

of the function of motion processing areas in the brain, including area MT. A corresponding measure of ventral stream function is the *form coherence* task, which tests the ability to perceive a circular shape, composed of short line segments oriented at a tangent to concentric circles, amongst randomly oriented line segments. This task has been previously used as a measure of ventral stream function (e.g Atkinson *et al.* 1997). Braddick *et al.* found that independent, but contiguous areas in both ventral and dorsal streams were preferentially activated by these stimuli.

1.4.4. Evidence that complicates the simple picture.

Jeannerod (1997) sees the idea of a simple dissociation between a dorsal stream subserving action and the ventral stream subserving object perception as being too clear-cut:

Firstly, there is some evidence to suggest that the object-orientated behaviour in patients with visual form agnosia may not be fully preserved. In other words what is preserved in DF is not a fully functioning system for visuomotor transformation, but a subsystem which produces automatic responses in conditions of impoverished input. Perenin and Rossetti (1996) report on a patient (PJG) with hemianopia of the right visual field. Objects were presented in the hemianopic field. The patient was asked either to produce movements toward the objects or to match the size or orientation of the same objects. In the reaching task, orientation and grip aperture were adapted to object properties, whereas in the matching task, there was no correlation between object orientation and the orientation of the hand or between object size and grip aperture. However, this patient's lesion was not in ventral stream areas, but in V1. According to Jeannerod (1997) this means that the preserved object oriented behaviour in Perenin and Rossetti's patient PJG (and maybe in DF too), is due to preserved subcortical connections to the dorsal system. He proposes that DF and PJG are using a ' primitive

system for fast and crude reactions to visual stimuli, that may only operate in situations in which there is time pressure, or where there is decreased awareness'. PJG was unable to make correct responses to object size or orientation in the blind hemifield when a delay was imposed between stimulus and movement. (Jeannerod, 1997). Evidence against this view is that DF is able to experience an orientation-contingent colour after-effect (Humphrey *et al.* 1991). As there is no evidence of colour processing in subcortical pathways to the dorsal stream, this would suggest DF's preserved abilities are not purely sub-cortical in origin (Milner and Goodale, 1995; p.135).

Secondly, there is PET evidence from Faillenot *et al.* (1997) which shows increased rCBF in *both* IT and PPC during object matching tasks (see below).

Thirdly, Jeannerod *et al.* (1994) present evidence for a contribution of the ventral stream to prehension in a patient with with optic ataxia. The patient showed impaired matching of grip size to objects, but was similar to a normal control on a perceptual size-matching task. The patient's performance improved, however, when familiar objects of similar size and shape to the 'neutral' objects used in the first experiment were used, suggesting that recognition/perceptual processing of form was intact and that information from object recognition aids visuomotor transformation.

1.4.5. A model of neural pathways underlying reach and grasp movements

Figure 1.4 shows the Fagg and Arbib model of how the grasping process is implemented in the brain. This model assigns a key function to area AIP as a point at which the ventral and dorsal streams interact in the processing of object affordances. In this model, visual input is passed to area PIP (referred to as cIPS in the discussion of Taira et al's study above), where different classes of objects are represented. The object classification is then passed to area AIP, where a set of possible grasp configurations are calculated. Input from area IT provides default grasp parameters for

familiar objects in pathological cases where input from the dorsal stream is disrupted (see section 1.4.4.). In the normal case, this link between the ventral and dorsal streams may alter the calculation of an appropriate grasp in the light of the context of the action (for example, in choosing between the different grasps afforded by a stick and a pencil of the same diameter). As reviewed in section 1.2.2, it is thought that the set of possible grasps for a given object is passed to area F5, where a final selection is made.

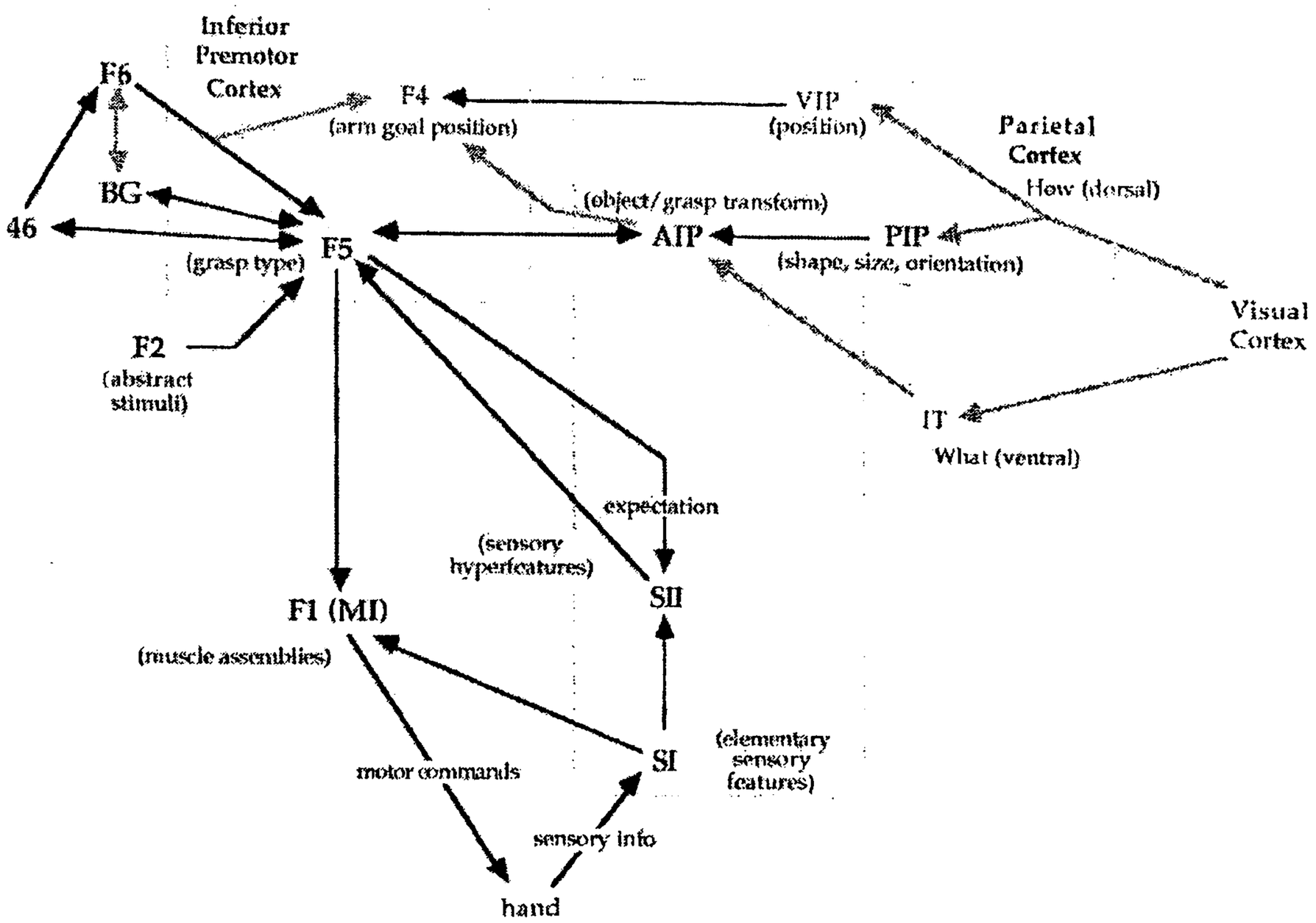


Figure 1.4. Model of neural pathways underlying reach and grasp movements, (From Fagg and Arbib, 1998)

PIP: posterior intraparietal cortex (also referred to as cIPS). AIP: anterior intraparietal cortex. VIP: ventral intraparietal cortex. BG: basal ganglia. SI, SII: somatosensory cortex. MI primary motor cortex.. IT inferotemporal cortex.

1.5 SELECTION FOR ACTION

The evolutionary function of the various processing streams described above is to accurately adapt the reach and grasp to the properties of the selected target. However, it is rare for there to be just one potential target for action in the visual field. We are usually presented with a complex array of different objects and must therefore first select between alternative targets, and then accurately specify the action according to the properties of the chosen object. This creates what Allport (1987) has termed the selection for action problem. Neumann (1990) has divided this problem into two components, selecting the how to perform an action (*parameter specification)* and selecting between alternative actions (*effector recruitment).* Parameter specification refers to the selection of appropriate parameters to control an action towards a single target, for instance the extent and direction of an arm movement and the time at which the hand starts to close when catching a ball. Neumann believes that this form of selection for action takes place automatically in dedicated control structures without the need for ongoing visual attention.

'In neural terms one may think of such control structures as systems of interconnected neurons, extending from the analysis of sensory input to the innervation of motor control units; that by means of specific neuronal connections, translate specific stimulus properties into specific action parameters'.

Jeannerod (1984) has proposed that the reach to grasp movement in man is controlled by 'visuomotor channels' with just these properties. Whilst such mechanisms are intrinsically selective, in that they only accept as input those parameters that are

directly relevant to their output, they are unable, in Neumann's view, to cope with the situation where there is more than one potential target for action.

In order to solve this kind of problem, of what to do rather than how to do it, an attentional mechanism is needed which determines which environmental information will act as the input to the control structures that specify action. What structures in the brain are involved in the two processes? The research reviewed above (section 1.4) suggests that the dorsal stream, in conjunction with premotor areas, is responsible for parameter specification. In other words, once the target has been selected, dedicated control structures translate visual input into motor commands which drive a saccade, or adapt the reach and grasp movement to the properties of the object chosen. (In some cases, such as a saccade to a suddenly presented stimulus, the operation of a control structure may be mandatory. This is what Neumann calls selection without attention.)

Object selection, on the other hand should involve ventral stream structures involved in object recognition. Recent research with adult humans (Deubel *et al.* 1998; Meegan and Tipper,1999, Castiello, 1996), and monkeys (Goldberg and Segraves, 1987), suggests that where subjects are presented with an selection of objects, all objects in the array are processed as potential targets for action in the dorsal stream. When a target is selected by identity-selection processes, which involve both the ventral stream and prefrontal cortex (Chelazzi *et al.* 1993), competing motor representations must be inhibited, or the selected representation enhanced in order to initiate action towards the desired object (Meegan and Tipper, 1999).

What about the ability *to select* an object on the basis of its grasp affordances, as opposed to adapting the grasp to those affordances once the object has been selected and an action initiated? As a recognition process, this might seem to need ventral stream information. In this case, the attended object would be compared with stored

representations, either derived from recent experience with the experimental objects or perhaps of prototypical graspable objects. If the object is recognized as graspable, then control structures in the action stream are set in train to initiate and specify the parameters for an action towards the chosen object. However, Castiello (1999) proposes that the parameters for action are only prepared for attended objects. It is therefore possible that giving attention to (and therefore implicitly preparing action towards) an object could also result in action stream information about affordances being delivered to target selection mechanisms, without the need to access stored representations. This suggestion is supported by Fagg and Arbib, (1998; see also Rizzolati, 2000) who propose that when an object is presented, a set of potential actions are prepared towards that object in area AIP and that the choice of action to the attended object is determined by in area F5. The developmental implications of this possibility are that the specialization of dorsal stream units for the computation of object affordances would be critical not just for the online control of action, but also for the basic ability to parse the visual world into objects that do or do not afford action.

1.6 THE DEVELOPMENT OF PREHENSION IN INFANTS.

The mature pattern of prehension is not reached in children until the second year of life. However, even newborn infants show signs of directed arm movements towards objects (Hofsten 1982). Some researchers have claimed that signs of early reaching movements reflect an innate organization of the motor pathways which subserve reaching. How does this ability develop in the first months of life? As noted above, the ability to reach for an object develops before the ability to grasp objects successfully (Hofsten,1989). This may reflect differential rates of maturation of pathways that control independent hand and finger movements (Kuypers, 1962). Alternatively, the

processing of object attributes necessary to grasp an object may be more complex than that for a reach, especially as a successful grasp may depend upon the coordination of two separate visuomotor channels.

1.6.1. Reach development in neonates

Bower, Broughton and Moore (1974) claimed to have demonstrated the existence of aimed reaches in neonates. However, attempts to replicate this study were unsuccessful (Dodwell, Muir and DiFranco,1976; Ruff and Halton, 1978). Trevarthen (1984) also describes aimed reaching in very young infants. He presented small objects at eye level to infants between one and two weeks of age. He observed that infants tracked the objects with coordinated head and eye movements, and also reports that infants made small hand and arm movements towards the objects. On occasion these movements resembled a fluid reach-to grasp movement, with maximal finger aperture occurring at the point at which the wrist achieved maximum height. He proposes that these movements are a pre-functional expression of a preformed motor program for prehension, which may even be present in the fetus. Trevarthen (1990) suggests that this 'pre-reaching' is (a) a primitive form of the mature reach and grasp movement, and (b) related to neural programs which evolved to organise cyclical sequences of movements in other vertebrates.

However, as Trevarthen himself admits, 'pre-reaching' could also be elicited by stimuli other than objects, such as sounds, and were often spontaneously performed with no obvious triggering stimulus. It was not until the three-dimensional characteristics of neonates' movements were studied by Hofsten (1982) that convincing evidence of aimed movements towards objects in neonates was provided. Hofsten found that forward extensions of the arm made when the object was fixated showed a smaller deviation from target direction than those movements initiated without fixation of the

target. This implies that visual and proprioceptive maps of space are at least partly in register at birth. Hofsten contends that this early linking of looking and reaching has an attentional rather than manipulative function. "When the neonate looks at and reaches for an object, both the reaching and the looking are parts of the same orienting response toward the object." (Hofsten, 1982) However, it is possible that these 'pre-reaching' movements are be an adaptive precursor to visually guided prehension (Trevarthen, 1974).

1.6.2. Kinematics of the developing reach

Hofsten (1979) divided infants' movements according to phases of acceleration and deceleration into "functional units", consisting of one acceleration phase and one deceleration phase. This follows a classification system used on monkey movements by Brooks (1974). The assumption is that each movement unit is programmed in advance and cannot be revised until it has been completed and feedback of the resulting hand position has been received. Adult reaching movements typically consist of one movement unit (see section 1.1 and Figure 1.1). Hofsten (1989) has charted four main changes in the characteristics of reaching between the ages of 19 to 31 weeks. It should be noted that Hofsten's results are based upon infants reaching to an object placed at nose height, so infants are effectively reaching upwards to contact the object.

1. The order of 'functional units' started to approximate that of the adult reach. The first phase of movement towards the object was more likely to be the longest by the end of this period than at the beginning.

2. The proportion of the movement taken up by this initial 'transport phase' grew from 46% to 69% during the period of the study.

3. The number of units in a reach declined

4. Reach trajectories straightened out. (Straightness measured as distance covered during a reach, divided by the shortest distance between the ends).

Why should infants' early movements be planned as a series of small sub-movements? Berthier (1996) has proposed that for young infants there is a lot of uncertainty in the outcome of any particular motor command. In this situation the optimal strategy is to move in a sequence of several sub-movements. However, Mathew and Cook (1990), have questioned the assumption that infant reaching movements are a sequence of ballistically aimed sub-movements, and present evidence for within-segment corrections. Reach trajectories from infants between 4.5 and 7 months were analysed. Whilst points of lowest hand speed were associated with change in direction of movement towards the target, it was also found that, within movement sub-units, trajectories were curved towards the target.

This suggests that continuous correction of the movement was taking place, especially as movements veered towards the target from a variety of starting directions. However, it is also possible that motor synergies for straight reaching may be immature. Out *et al.* (1997) also claim that multiple segment reaches do not consist of discrete sub-movements, but result from inadequate compensation for the natural tendency of the arm to oscillate. However some researchers, working from the 'dynamic systems' perspective contest the idea that the stereotypical pattern found in mature reach trajectories is an expression of an innate program for reaching such as that proposed by Trevarthen. For example, Thelen (1998; see also Sporns and Edelman, 1993) contrasts this view of motor development as an 'inside out' process, where maturation of the required neural substrate is the main factor which drives motor development, with an alternative view which takes much more account of how the protracted and complex process of learning to reach determines neural development. Konczak and Dichgans (1997a,b) have carried out a longitudinal study of reaching movements in infants aged 4 to 36 months. Using the Elite system, they recorded reaching movements to single objects, which were presented at shoulder height and to the right hand side of the infants. Elite markers were placed on the elbow and shoulder as well as the hand, which allowed them to analyse the

kinematics of the reach trajectory, angular kinematics and intersegmental dynamics (see note above on biomechanics).

Reach kinematics. Between 16 and 24 weeks, the number of movement units in the reach decreased, hand paths straightened and movement time decreased dramatically. Between 24 weeks and 2 years these parameters converged gradually towards adult-like levels. Konczak *et al.* characterise this developmental sequence as a period of rapid improvement in the 5 weeks following reaching onset, followed by an extended period of 'fine-tuning' between 24 weeks and 2 years of age.

Angular kinematics. In infants up to 2 years of age, the onset of shoulder flexion and extension of the elbow was not set into a consistent timing pattern. Elbow extension could either precede or follow shoulder extension. After 2 years, and in adults, a pattern emerged where shoulder flexion reliably preceded extension of the elbow. When joint kinematics and hand paths were compared in infants aged 9 – 15 months and adults, it was evident that although hand paths in infants and adults were similar they were being produced by different patterns of angular displacement of the elbow and shoulder. This implies that infants at this age have not yet arrived at a stable solution to the degrees of freedom problem (Bernstein, 1967). (The degrees of freedom problem arises from the fact that, given a multi-jointed arm, a movement to a target can be accomplished in an infinite number of ways.).

Joint forces. A developmental trend was also observed in the relative timing of maximum joint torques, as would be expected from the kinematic measures. The point in the reach at which the peak muscle torque was produced at the elbow was initially very variable, with a mean of 50 % of total movement time at 20 weeks. This value decreased to a near-adult level (28%) in the next three months.

Thelen, Corbetta and Spencer (1996) carried out a longitudinal study of reaching movements in four children to a single object presented at shoulder height. Kinematic and electromyographic measurements were taken once a week from 3-30 weeks and once every two weeks between 30 and 52 weeks. In the 1996 study they report on measurements taken in the 2 weeks before and after the onset of reaching (the first week in which each individual infant consistently contacted a toy presented to them. Each infant achieved this skill at different ages; 11, 15, 21 and 22 weeks. Thelen *et al.* could find no evidence that a pre-reaching pattern is transformed into a mature reach. Rather, for each infant, reaching emerged from a different pattern of background motor activity. Two infants displayed a typical pattern of forceful movements, which had to be damped down to achieve successful reaching, whereas two quieter children had to generate faster and more forcible movements. The first successful reaches in the more active infants were 'high speed swipes' whereas those of the less active infant were slower with more controlled trajectories. Thus, the development of controlled mature reach trajectories for these infants involved different modifications of initially successful strategies. In Thelen et al's words reaching 'posed a different dynamic and biomechanical problem for each child'. Different 'motor sets' gave rise to different patterns of interjoint coordination, reach trajectories and distribution of forces governing the reach.

The infants also did not show a smooth transition to a mature reach pattern. Each had periods of improvement in accuracy and efficiency of the reach, followed by periods of instability and poor control where a pattern of faster movement was observed in both reaching and non-reaching movements. (Thelen suggests that infants may simplify the reach by 'freezing out' degrees of freedom in the arm , for instance by locking the elbow joint. When this is released there may be a period of instability

whilst the greater potential variability in the movement is coped with). All infants settled into a pattern of improved reaching between 30-36 weeks, 'with little further improvement by the end of the first year'. Konczak et al's finding that stereotypical reach kinematics are not displayed until 2 years is based upon his finding that the variability in reaches continues to decrease after the first year of life. At 1 year Thelen's four infants showed an average of between 1.4 - 1.88 movement units in their reaches, whereas the velocity profile of the adult reach is typically unimodal (i.e. consists of 1 movement unit). Konczak reports that one-third of reaches at 15 months showed a unimodal velocity profile; by 2 years this proportion was over 75%.

1.6.4. Grasp development

In neonates, the hand tends to open during arm extension, whether or not the infant is looking at an object. (Hofsten, 1982). However, around the age of 2 months this coupling of arm and hand movements starts to break up. Hofsten (1989) reports that infants at 2 months started to close the hand as the arm extended, again whether or not the infant was looking at an object. By 3 months, infants are starting to open the hand during reaching, in response to the presence of an object. By 5-6 months the infant is able to successfully reach out and grasp an object.

Grasping an object requires

1. That the hand be correctly configured according to the *size* and *orientation* of the object.

2. That the closing of the hand be accurately timed; the movement is more efficient if the grasp starts in anticipation of, rather than as a reaction to, contact with the object.

Adaptation of the grasp to object size

Hofsten and Ronnquist (1988) compared both the timing of grasping movements and the relation between hand aperture and object size in adults and infants at 5-6 months, 9 months and 13 months. They showed that all the infants were capable of anticipatory grasping; however, the younger infants (between 5-6 months) started to close the hand earlier than older infants and adults. Hand aperture was geared to the size of the object only in the older infants and adults. However, as Hofsten points out, this result may simply reflect the fact that hand aperture was measured between the ends of the thumb and forefinger. (Infants at this age do not primarily use the ends of the fingers when grasping objects but tend to grasp objects with the palm and the bottom part of the fingers.)

Infants may be able to compute the grosser characteristics of objects, i.e. whether they are too big to pick up, before they are able to accurately calibrate grip size to object size. One way to test this is to observe the presence or absence of a reach towards a single presented object. Here the underlying assumption is that if more reaches for 'graspable' objects are observed, then grasp-relevant object properties are influencing whether or not the infant attempts a reach. Another means of determining whether infants are able to adapt the grip to the characteristics is to observe the kinds of grip that infants use when grasping objects of different sizes.

Halverson (1931) filmed infants aged between 16 to 52 weeks whilst grasping a 1 inch cube. He proposed that there was an orderly developmental transition in the grip configurations used by infants; from the predominant use of grips involving the underside of the fingers and the palm of the hand ('power' grips) to grips involving opposition between the thumb and one or more fingers ('precision' grips), starting at around 20 weeks. Butterworth *et al.* (1997) have

carried out a partial replication of Halverson's study. They presented 37 infants between 24 and 83 weeks with spheres and cubes, measuring between 0.5cm to 4 cm across. The objects were presented one at a time suspended on string in front of the infants and. Infants were grouped into 4 age groups, 6-8, 9-11, 12-14, and 15-20 months. Halverson's finding that the number of power grips used by the infants decreased with age was replicated. Infants in all age groups also used more fingers in the grasp as object span increased. However, this study does not provide clear evidence that infants are able to use *visual* information to specify the grip, as Butterworth *et al.* do not report on whether the grip was prepared in advance of contact with the object. Newell, Scully, McDonald and Bailleargeon (1989) have demonstrated that in infants as young as 4 months there is a systematic relationship between the size of the object and the number of fingers recruited in the grip (see also Newell, McDonald and Bailleargeon (1993). However, the ability to use visual information to specify the number of fingers used in the grip seemed to develop later. Only in infants at 8 months was there clear evidence of the grip being prepared in advance of contact with the object.

Siddiqui (1995) has carried out a study that observed both the kinds of grip used and the frequency of reaches to objects of different sizes, ranging from 0.5cm to 14cm in diameter. She reports that infants as young as five months are able to use different grip configurations according to object size; and that they use visual information to do this. Younger infants were less likely to reach for the smaller objects. Also the number of grasps using two or three digits increased significantly with age, as the number of whole hand grasps decreased. Siddiqui believes that this increase reflects the increasing availability of differentiated finger movements as the corticomotoneuronal tract matures. Infants may be able to

perceive grip-relevant object characteristics before they are able to reliably form a grip, as reaches to smaller objects were more likely to be made with just the thumb and first two fingers at all ages. (But see Watts, Eyre, Kelly and Ramesh, 1992 in section on pyramidal tract below).

Newell, Scully, McDonald and Baillеargeon (1989) have demonstrated that in infants as young as 4 months there is a systematic relationship between the size of the object and the number of fingers recruited in the grip (see also Newell McDonald and Baillеargeon (1993); Butterworth, Verweij and Hopkins (1997)). However, the ability to use visual information to specify the number of fingers used in the grip seems to develop later. Only in infants at 8 months was there clear evidence of the grip being prepared in advance of contact with the object.

Adaptation of grasp to object orientation

Lockman, Ashmead and Bushnell (1984) studied this problem in 5 and 9-month-old infants. The infants were presented with horizontal and vertical rods, and the point at which the hand started to orient itself to the object was measured. It was found that anticipatory hand orientation occurred only in the 9-month-old babies, whereas the younger infants tended to adjust the hand after contact with the object. However, Lockman *et al.* used a rather crude means of measuring hand orientation, which may have missed subtler adjustments in orientation. Hand orientation was coded from video records, at only four points during the reach, using a four point scale, ranging between 0 to 90 degrees in increments of 22 ½ degrees. Hofsten and Fazel-Dandy (1984) studied the adjustment of the hand to the orientation of an object in infants 18-34 weeks old. They measured orientation at 60 ms intervals during the last 540ms of the reach. Their results show incomplete attempts to orient the hand correctly are present in infants at 5

months. (11/15 infants showing difference in mean hand orientation in the direction of object orientation; results pooled between infants at 18 and 22 weeks).

1.6.5 Previous work in the Visual Development Unit

Previous experiments in the Visual Development Unit have used the Elite motion tracking system to study infant reaching. Braddick *et al.* (1996) examined the role of binocular disparity cues in the control of reaching in infants aged 6 – 9 months. Results showed that there were more movement units in the reach, and a higher peak velocity, when infants reached with one eye covered than when they were allowed to use two eyes.

King *et al.* (1997, see also King 1998) studied preferential reaching to natural objects of different sizes, and preferential looking to representations of similar objects, displayed on a computer screen in four separate samples of infants, aged between 6 and 15 months. (King *et al.* 1997, King, 1998; experiments 2-5) The kinematics of reach trajectories were also measured. King *et al.* (1997; experiment 2 in King, 1998) used two object sizes (6cm and 2.5cm diameter). The largest object was too large for infants of this age to grasp. The medium sized object comfortably fitted the hand size of most of the infants in the study. King, (1998; experiments 3 and 5) used an additional, smaller cylinder (1 cm diameter) to test the effects of the increased precision needed to grasp it on reaching preferences and kinematics. In the following discussion these objects will be referred to as L (large object), M (medium object) and S (small object).

A number of findings have come from the studies of King *et al.* Firstly, in experiments where infants are restricted to reaching with one hand, there is a strong bias to reach to the object on the same side as the reaching hand. Secondly, there is a consistent pattern of reaching preference for graspable objects, measured as a greater proportion of contralateral reaches when a smaller object of the pair is on the contralateral side. In

experiment 2, where only the large and medium objects were used, the preference was for the medium object. In experiments 3 and 5, where three object sizes were used, infants in all age groups tested showed a preference for the small and medium object over the large object. In experiment 5 younger infants showed lower peak velocities and longer movement duration when reaching to the smallest object.

Looking preferences (experiments 4 and 5) were quite sensitive to the exact placement of the objects. It should be noted that these experiments used different age groups and sample sizes. Experiment 4 used a group of 10 infants aged between 6 ½ - 10 ½ months, whereas experiment 5 used two groups of 15 infants aged between 5-8 months and 8-12 months. In both experiments, there was a significant preference for looking first at the large object, in the LS pairing, in trials where objects were placed with their *centres* equidistant from the fixation point. Of course, in this condition, the edge of largest object is closest to the fixation point and is therefore more likely to be fixated first. Where retinal eccentricity was controlled for, and the objects were shown on the computer screen with their *edges* equidistant from the fixation point, results were less clear-cut. A significant preference for M over L was observed in experiment 4 and in the younger age group in experiment 5. However, this preference was reversed in the older age group in experiment 5. A possible interpretation of these results is that two visual orienting mechanisms operate in parallel in young infants. One mechanism is more reflexive and orients to the stimulus which occupies the largest area in the visual field. Another has the capacity to use higher-order information that is relevant to prehension, and will fixate first upon graspable objects if the more primitive mechanism is not triggered. However, the fact that older infants in experiment 5 looked first at the Large object, even when eccentricity is controlled for, cannot be explained this way. Object-related looking behaviour in infants of this age therefore requires further

investigation. An important point to note is that even though that the images displayed on the screen were constructed to be as realistic as possible, there may be important differences in infants' looking preferences when they are presented with real objects, rather than two-dimensional representations.

1.7 UNDERLYING NEURAL DEVELOPMENT

The reach and grasp components of prehension may develop at different rates. Infants will launch a reach towards an object before they are reliably able to form an appropriate grip in advance of contact with the object. When studying infants' ability to use visual information to predict the 'graspability' of an object an important question to ask is whether the requisite circuitry is in place for the finger movements necessary for a small object to be grasped. The following section therefore considers the development of the corticospinal tract, which projects from the motor cortex to the spinal cord. This tract of nerve fibres is not fully myelinated at birth, and is thought to be essential for the development of fine finger movements.

1.7.1. Development of the pyramidal tract in primates

It is commonly accepted that the development of the pyramidal tract is an essential prerequisite for differentiated finger movements. Monkeys with experimentally induced lesions of the pyramidal tract are unable to retrieve small food items from wells in a test board (Lawrence & Kuypers, 1968). Armand *et al.* (1994) studied the development of corticomotoneuronal (CM) projections in macaque monkeys. They injected a tracer chemical into the hand area of motor cortex and studied the pattern of connections in the area of spinal cord which supplies hand and finger muscles. They found that in the adult there was a dense set of connections in this

area. However, connections in 5-day old monkeys were sparse. By 2 ½ months, a similar pattern of connectivity to that in the adult was established. This is the age at which independent finger movements are first observed in the macaque (see Lawrence and Hopkins, 1976 cited in Armand *et al.* 1994). However, labelling was less dense, and had not reached adult levels even in the 11 ½ month old monkey.

In humans myelination of the tract may take at least 2 – 3 years. (Yakovlev and Lacours, 1967). Brody *et al.* (1987) have examined the extent of myelination in infant brains at post-mortem, and found that it was still 'far from complete' at 2 years. Eyre *et al.* (1991) used the latency of responses evoked by trans-cranial magnetic stimulation (TMS) to infer the level of development of the PMT. They report a period of rapid reduction in motor conduction time during the first two years, after which it remained constant until adulthood. However, the distance from the brain to the arm increases as the child grows to adult size. This result therefore implies the conduction velocity must increase as the body grows, with the process of maturation not reaching completion until about 16 years of age.

However a behavioural experiment complicates the picture slightly. Watts, Eyre, Kelly and Ramesh (1992) carried out a longitudinal study on 20 children, testing for the development of pincer grasp and relatively independent finger movements. Measurements of conduction time using TMS were also taken. They used a task similar to that used by Lawrence and Hopkins (1976), in which small food items are retrieved from wells in a test board. In all but one subject the ability to 'winkle out' small pieces of chocolate from the board was observed before the rapid reduction in conduction time had taken place. (A reduction in conduction time to adult values occurred at different ages in different infants, between 6 and 15 months). This indicates that the rapid

reduction of conduction time observed using TMS may not be a reliable indicator of functional connectivity.

1.8 THE CONTROL OF EYE MOVEMENTS

The research described so far has concentrated upon the subdivisions of cortex related to arm movements. However, a number of cortical and sub-cortical systems have also been identified which are involved in the control of eye movements. In addition, it has been discovered that some neurons in the parietal reach region (the medial part of PPC) are also active during saccades (Snyder *et al.* 2000).

1.8.1 Circuits controlling eye movements.

The main neural pathways involved in visual orienting are depicted in Figure 1.5. (see Johnson, 1997, Atkinson, 2000 for reviews). It is important to differentiate between different kinds of eye movements. Some eye movements, such as optokinetic nystagmus, are involved in maintaining a stable retinal image in the presence of a moving visual field. Other eye movements are closely related to shifts in attention, whether reflexive or voluntary. *Reflexive eye movements* (the rapid shift of fixation towards a suddenly appearing stimulus) are controlled by a subcortical pathway that passes from the eye to superior colliculus. Another kind of eye movement takes place when one is voluntarily looking from one object to another. These *endogenously driven saccades* are controlled by a pathway which passes from striate cortex via the lateral geniculate nucleus (LGN) and parietal cortex to the frontal eye fields. Another pathway, running from the eye to the superior colliculus via LGN and area MT is

involved in the control of the *pursuit eye movements* which take place when tracking a moving object. Lastly, a pathway involving a sub-cortical loop via the basal ganglia is

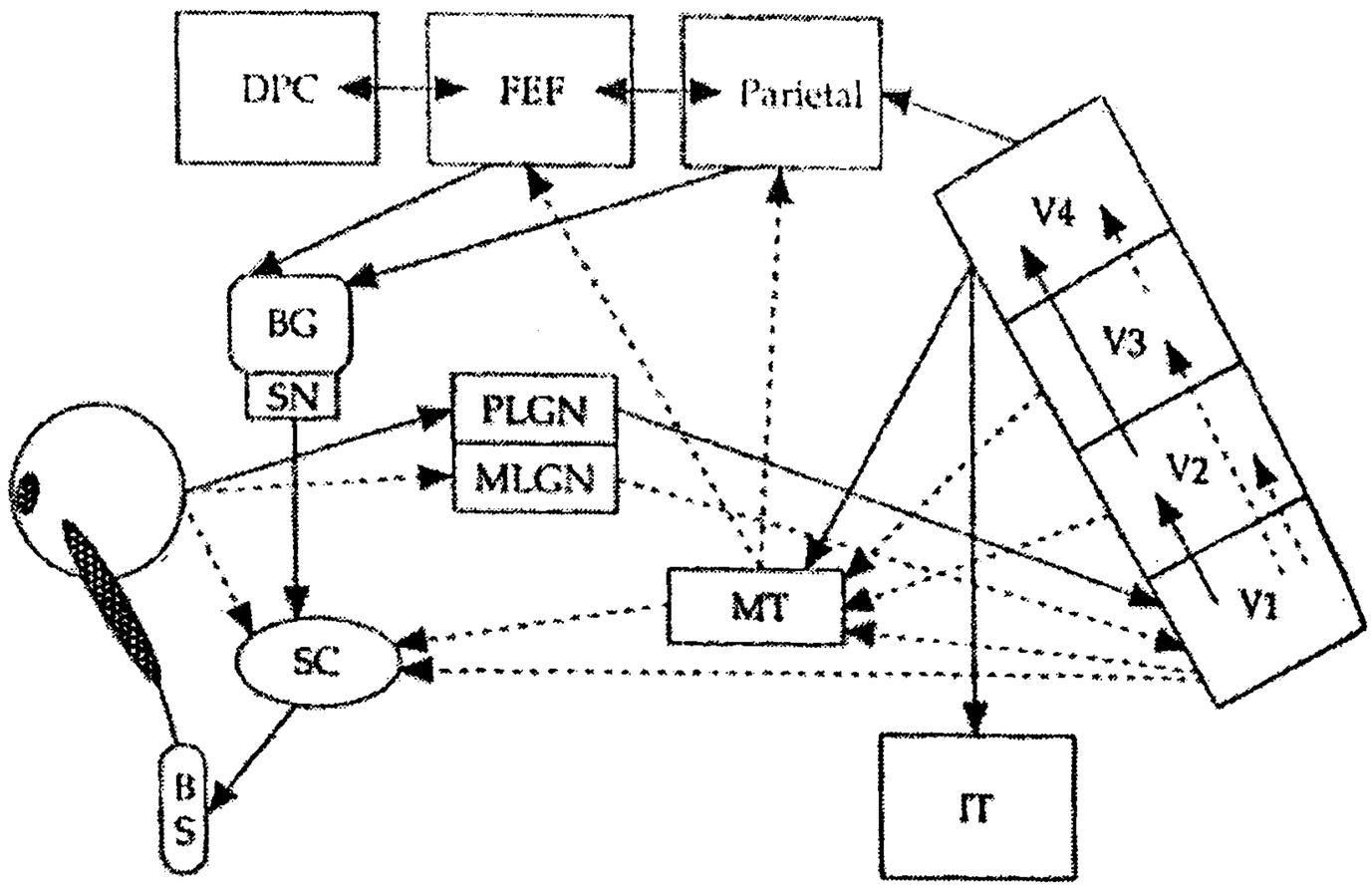


Figure 1.5 The main neural pathways involved in visual orienting. (Reproduced from Johnson, 1996). See text for details.

thought to enable cortically mediated modulation of reflexive eye movements (Johnson, 1997).

1.8.2 Are eye and arm movements 'yoked'?

It is clear that eye and arm movements are functionally linked during prehension, as the gaze typically shifts to the target object just before a reach (Biguer *et al.* 1982). However, Carey (2000) has reviewed a group of studies which suggest that the link between eye and arm movements may go beyond that necessary to identify a target for an impending reach. For instance, Fisk and Goodale (1985) have shown that both hand and eye movements to targets contralateral to the reaching hand were some 40-50 ms slower than to ipsilateral targets. This is despite the fact that (a) they did not

take place at the same time, as eye movement latencies are faster than arm movement latencies and (b) eye movements, unlike arm movements, are similar regardless of which side of the body the target lies.

This linkage between eye and arm movements has also been identified at the neural level. Recent experiments by Snyder *et al.* (1997; 2000) have identified a subset of cells in the parietal reach region (PRR; the medial part of PPC) which are involved in the preparation of a reach (i.e. increase their firing rate during a delay period before a reach), but are not involved in the preparation of saccades. These cells nevertheless fired at the time of a saccade, during a delayed saccade task. Snyder *et al.* propose that the activity of these cells may reflect actions that are automatically activated, but not carried out. Because reaches and saccades are often performed towards the same stimulus, there may be a default motor plan which links them elicited by the appearance of a target. As Snyder *et al.* put it,

"Whenever the eyes are moved, a plan is formed in PRR that would carry the arm to the same target. On a delayed saccade trial, this plan is then suppressed somewhere between PRR and the motor output. In this view, the activity in PRR during a saccade is a manifestation of cross-coupling between reach and saccade pathways."

Independent activation of reaches and saccades may therefore depend upon a pattern of inhibition between neurons in these closely linked motor pathways. The effects of a pathological inability to inhibit this linkage may be seen in the case of Ms D, reported by Carey *et al.* (1997). This patient, in whom the parietal lobes on both sides of the brain had atrophied, was unable to reach for a target that she did not simultaneously fixate. Carey *et al.* report that this patient would reach to the place she

was looking at, then apologise as she knew she had reached to the wrong place, but then proceed to make the same error again and again.

There is also some evidence for a linkage between eye and arm movements in the smooth pursuit system, where tracking movements of the eye are more accurate when the hand also tracks a visual target (Gauthier *et al.* 1988) and also at the sub-cortical level where Werner *et al.* (1997) have demonstrated the existence of arm-movement related cells in the superior colliculus. Werner *et al.* speculate that SC may be involved in a general orienting system which involves arm movements as well as eye and head movements.

1.7 SUMMARY AND CONCLUSION

Visually guided prehension in infants starts at around 4 months, and from this age infants reach readily for objects which are within range. From the pioneering work on infant reaching carried out by Claes von Hofsten and Esther Thelen, we know that by 31-36 weeks, the kinematic characteristics of the reach are starting to resemble those of the adult, (Hofsten, 1991; Thelen *et al.* 1996), although stereotypical patterns are not observed until the second year of life (Konczak and Dichgans,1997).

Reaching out for an object and grasping it poses two distinct computational problems for the developing motor system. To reach accurately towards an object involves encoding its location. Here the parameters most relevant to visuomotor programming are the direction and amplitude of the necessary arm movement (which may need to be co-ordinated with trunk movements). To grasp an object, on the other hand, requires coding of the intrinsic features of an object, such as its size, shape and orientation (Arbib, 1985, Jeannerod, 1988). Both the eye

movements involved in the visual acquisition of a target object, and the subsequent transformation of visual information about objects into appropriate motor commands are thought to be controlled by the 'dorsal stream' of visual processing, a network of specialised areas in the parietal lobes (Milner and Goodale, 1995; Rizzolati *et al.* 1997). These parietal areas are in turn selectively connected to areas of the frontal lobes, forming a set of 'parietofrontal modules' involved in the control of reaching, grasping, and eye movements.

These specialised input–output channels seem to be sub-divisions within a broader partitioning of function within the primate brain. Two diverging pathways from primary visual cortex have been mapped in the visual system. The ventral stream, passes to infero-temporal cortex, the dorsal stream passes to posterior parietal cortex. (Ungerleider and Mishkin (1982). Evidence from normal performance, human neuropsychology and monkey physiology supports the proposal that these two systems have evolved to transform visual information for different purposes. The dorsal stream is thought to deal with the 'online' control of action. The ventral stream, by contrast, is thought to deal with the identity and significance of objects. Of course, when selecting an object from those available in the environment as a target for manual action, information from both streams may be necessary. Ventral stream information may be used to recognise familiar objects, or to modify the grip according to the intended use of the object, whereas in the dorsal stream, a limited subset of visual information is used to activate the appropriate motor schemas which go to make up the reach and grasp movement. (Fagg and Arbib, 1998). One influential model of visuo-manual processing (the Fagg, Arbib, Rizzolati, Sakata, or FARS model, see Arbib, 1997) assigns a key function to an area within the dorsal stream (the anterior intraparietal sulcus) in

specifying grasp “affordances"; both directly, from grasp-related object parameters such as size and orientation, and more indirectly through connections with areas of the ventral stream (inferotemporal cortex) dealing with object recognition (it should be noted that in the FARS model, the term affordances is not used in a strictly Gibsonian sense). Thus, there is neurophysiological evidence for distinct but interlinked visuomotor modules underlying reaching and grasping in adult primates (Milner and Goodale, 1995). However, it is not known whether object processing in the visual system is from the outset divided in this way, or whether the modularisation of visuomotor pathways only occurs as the transformation of visual information into motor commands becomes more practiced.

Chapters 3 and 4 of this thesis report on an investigation of reaching and looking preferences in infants between 5 and 15 months. If the development of reaching in infants reflects the development of a specialised visuomotor system, then it is possible that the visual properties which drive reaching may be quite different than those which drive fixations. This may have implications for the developmental time course of the ventral and dorsal streams. For instance, if infants are able to demonstrate a visual preference for objects which are suitable for grasping before they are able to demonstrate a similar preference in reaching behaviour, this would imply that ventral stream object recognition mechanisms are operating before dorsal stream action control mechanisms.

It should not be forgotten that there are at least 5 developing systems which can potentially influence eye and arm movements in infants (3 in the dorsal/parietofrontal stream for reaching, grasping and saccadic eye movements, a ventral stream object recognition system and also a system that directs orientation to suddenly presented stimuli; see Atkinson, 2000). Simultaneous observations of

looking and reaching behaviour made it possible to examine how these systems interact in determining motor output in infants.

Lastly, an alternative way of tracking the developing function of dorsal stream mechanisms controlling reaching is to track changes in the kinematics of reaching movements with age, and in response to different objects. Kinematic measures of infants reaches therefore were also recorded in the present experiments, using the Elite motion tracking system.

2 Methodology

This chapter will describe the methods used for the infant experiments reported in this thesis. Also included here is a description of the Elite motion tracking equipment, and an overview of kinematic analysis. Methods for the Williams syndrome experiments will be described in chapters 6 and 7.

2.1 MEASURES OF INFANT GRASPING

A number of different measures can be used to investigate infants' perception of grasp-related affordances (the 'graspability' of an object). Some researchers (e.g. Hofsten and Ronnquist, 1988) have measured the relation between maximum hand aperture and object size. However, the significance of measurements of grip scaling is uncertain in young infants. Infants may not use the same parts of the hand to grasp objects as adults, so measures of grip aperture may not be very informative. They may also, in the first phase of developing reaching, use a 'default strategy' of opening the hand to the maximum at the start of the reach.

An alternative method is to measure the type of grip that is used to grasp objects of different shapes and sizes. Whilst detailed measures of grip scaling may be difficult to obtain, the development of the ability to form an appropriate grip for the object can be used as an index of visuomotor maturity. Here the assumption is that a pincer grip is more appropriate for smaller objects, whereas a whole hand grip is more appropriate for larger objects. However, this assumption does not hold in all cases. Also, it is possible that infants may be able to compute the grosser

characteristics of objects, i.e. whether they are too big to pick up, before they are able to form a pincer grip, or to accurately calibrate grip size to object size.

One way to test this is to observe the presence or absence of a reach towards a single presented object. Here the underlying assumption is that if more reaches for 'graspable' objects are observed, then grasp-relevant object properties are influencing whether or not the infant attempts a reach.

However, none of the above methods permit comparable measures to be taken of how object properties such as size or visual pattern influence both eye fixation and reaching. To enable this, a new experimental methodology had to be designed which would allow the preferences of the looking and reaching systems to be compared, and which might also uncover interactions or linkages between the operation of the two systems.

2.1 SIMULTANEOUS PREFERENTIAL REACHING AND PREFERENTIAL LOOKING.

An established method of investigating infants' ability to make visual discriminations is the preferential looking technique. Here the assumption is that if a reliable preference is observed for one stimulus over another, then the infant must be discriminating between the two stimuli, and showing a visual preference for one of them. Taking advantage of the fact that infants between 5 and 15 months of age reach almost compulsively to objects which are presented to them, an analogous 'preferential reaching' paradigm was designed. Infants are presented with two objects, which vary on the dimension of interest, in this case size. If infants reliably choose to reach for objects which are of a size appropriate for their hands, rather than objects which are too large for them to pick up, it can be deduced that they are able to discriminate between

objects on the basis of grasp affordance. Thus, we have two measures of infants' ability to make visual discriminations, preferential reaching and preferential looking. However, whilst object size constrains the target of a successful reach, it puts no constraints upon looking direction. Consequently, an infant might find an object interesting to look at, even if it does not readily elicit reaches because its shape or size makes it difficult for a small hand to pick up. A previous study (King *et al.* 1996, King, 1998), had compared preferential looking to computer rendered representations of objects with reaching to real objects. However, whilst both measures were taken from the same infants in this study, the looking behaviour measured was not directly related to the reaching behaviour (although King *et al.* reported that infants did one some occasions try to reach for the computer rendered objects). In addition, it is possible that differences in looking and reaching preferences observed in this study were due to differences between the two kinds of stimuli. In the experiments reported here, therefore, reaching and looking behaviour was observed simultaneously for the same objects. This method allow inferences to be made about possible linkages and interactions between the different visuomotor subsystems involved in looking and reaching.

2.2 OVERVIEW OF KINEMATIC ANALYSIS

Important advances in the study of infant reaching have been made possible with the advent of motion analysis technology. Before discussing the methods specific to this thesis, I will give a brief overview of the methods and terminology of biomechanical and kinematic analysis.

2.2.1. Biomechanics

Biomechanics is the 'application of the principles of mechanics to the study of biological systems in motion' (Zernicke and Schneider, 1993). In mechanics, a division is made between *kinematics* and *dynamics*, that is between the study of different forms of motion and the causes for changes in motion. Thus, in the context of human movement, the kinematic variables such as velocity and acceleration represent the movement itself. Dynamic variables such as force and torque (force multiplied by distance from point of application), on the other hand, represent the underlying cause of that movement.

2.2.2. Kinematic analysis

The classic studies of Jeannerod in the 1980's were the first to give a detailed insight into the coordination of the reach to grasp movement. Using a frame-by-frame analysis of film records, Jeannerod and his colleagues were able to chart the typical features of a reach to grasp movement and to make inferences about its underlying organization. In the 1980s various motion analysis systems (MAS) were developed that could automate the data collection process in these studies (e.g. Elite, Selspot, Watsmart.) These systems give the researcher a record of the x,y,z co-ordinates of a marker attached to a particular limb segment at sampling rates of up to 300 hz, depending upon the system used. From this record can be derived a number of parameters that describe different aspects of the reach, including movement trajectory, velocity, acceleration and joint angles.

2.2.3. Psychological significance of kinematic measures

A major assumption in kinematic analysis is that information can be gained about the brain processes underlying movement from studying invariances in movement

trajectories. Marteniuk and MacKenzie (1990) have suggested three approaches to the analysis of kinematic data in adult subjects. Firstly, one can look for *kinematic invariances*. For instance, Jeannerod (1984) showed that when a subject makes reaches to the same object, placed at different distances from the body, maximum grip aperture remains constant. Conversely, one can measure *systematic variance*, the way in which kinematic profiles change to a new, invariant pattern under different experimental manipulations. For instance, the peak velocity of a reach tends to increase with movement distance. Lastly, it is possible to study *intra-individual variability*, which is calculated as the standard deviation of each individual's trials performed under a given experimental condition.

An additional level of analysis can be provided by calculating the dynamics of the limb segments involved, using knowledge of the mass of the limb segment, and the locations of their centre of mass.(see Zernicke and Schneider, 1993 for methods).

Movement duration and maximum hand speed may reflect the efficiency of the reach, in that a confident reaching movement, which has become automatic due to repeated practice, can be expected to take less time, and to carried out at a higher velocity than an unpractised movement. However, before the ability to grasp objects accurately and consistently is developed, young infants may use fast, single-segment reaches, in which the hand is launched towards the target without the deceleration and adjustment phases characteristic of adult reaches (Mathew and Cook, 1990). Differences in movement duration, maximum hand speed and deceleration time may therefore reflect age-related changes in motor programming. Increasing maturity of prehension has also been associated with a decrease in the number of 'movement units' in infants' movements, as indexed by the number of peaks in the hand speed profile

(Mathew and Cook, 1990, Hofsten, 1979). (See discussion of movement units in section 1.6.2).

It is also possible, using the Elite system, to measure the aperture of the hand as it approaches the object. Whilst in infants this is practically very difficult (and the significance of such measures have been disputed), in adults and older children it is possible to use this measure to gain some insight into the development and co-ordination of the two elements of the reach and grasp movement. In addition, motion analysis technology makes it possible to compare the functioning of the ventral and dorsal streams of visual processing, by comparing visuomotor and perceptual measures of object size perception.

2.3 KINEMATIC METHODS.

2.3.1. Elite system.

In the experiment reported here, a two camera Elite motion tracking system (BTS, Milan) with a sampling rate of 50Hz was used to create a kinematic record of infants' hand movements. Cameras were ceiling mounted with a separation of 1.35m., allowing an acquisition volume close to a cubic metre. The system was controlled by a 120mhz Pentium PC, which was also used to store and analyse the data.

Data files from each trial were transformed into a spreadsheet file containing position and instantaneous velocity for each marker, using software designed for previous experiments in this laboratory (King *et al.* 1998). For the present experiments, software was written in Labview (National Instruments) which enables the hand speed profile and the trajectory in the horizontal plane of each reach to be displayed, and the desired segment to be marked, using an interactive cursor display. The desired dependent variables are then written automatically to a data file for further analysis.

This arrangement enables the video record of a reach to be compared with a display of the velocity profile and trajectory.

2.3.2. Identification of reach initiation.

It is difficult to identify unambiguously the start of a goal-directed movement in infants. One cannot instruct them to start a reach at a particular time, or from a defined position. (See Corbetta and Thelen, 1995, for a methodological review). In the experiments reported here, the start of a reach was first identified from the video record, as the frame in which the hand started to accelerate towards one of the objects. This acceleration was usually accompanied by fixation of the target object, and closely followed by opening of the hand. Two timing measures were made: the time at which the reach was judged to have started and the time of first contact with the object were recorded on a spreadsheet file. The kinematic record for the reach was then displayed on screen, and the corresponding segment of the reach was marked, using the interactive cursor display. The start of the reach was then defined as the minimum in the speed profile that immediately preceded the initiation point identified from the video record. The direction of the reach could also be checked from the trajectory display. The end of the reach was defined as the time of first contact with the object. This was identifiable on the Elite record as a displacement in the object marker on the kinematic record.

3 The development of reaching and looking preferences in infants to objects of different sizes.

3.1 EXPERIMENT 1: INTRODUCTION

A pathological dissociation of ventral and dorsal streams is believed to occur when patients are able to make perceptual discriminations that they cannot translate into action. One might be able to demonstrate such a dissociation in the course of development if, for example, infants were able to make discriminations between objects on a looking measure, but did not demonstrate the same discrimination in their choice of a target for reaching (assuming that infants have attained the necessary level of competence in reaching). For instance, if a sensitivity to grasp affordances were innate, and reliable selection of graspable objects for reaching depended solely upon maturation of the online control of prehension, there might be a point in development at which infants would reliably look first, or longer, at graspable objects before they preferred to reach for them. A less specific hypothesis is that, in infancy, the systems controlling looking and reaching are preferentially driven by different stimulus variables.

To test these possibilities, infants in this study were given the opportunity in each trial to select one object from a pair, initially as a target for fixation and then as a target for a reaching movement. Whereas it was predicted that the reaching system would become progressively more attuned to visual inputs which signal the graspability of an object, it was an open question whether at each age, the looking system would be entrained by the grasp-related object attributes activating reaching, or whether it would

remain uncoupled from the visual control of reaching and be activated by a more general visual salience. Thus this study was intended to test the developmental trend in the degree of linkage between the two visuomotor control systems.

Recent research on selection for action suggests that where adult humans are presented with an choice of objects, all objects in the array are processed as potential targets for action in the dorsal stream. Target selection involves the inhibition of competing motor representations or the enhancement of the selected representation. A number of studies have also shown that information from flanking objects can perturb or delay eye movements as well as reaching movements (see section 1.5) Of course, infants cannot be instructed to attend to or reach for a particular target, as is possible in an adult experiment. However, by observing the sequence of looks and reaches in each trial it was hoped to gain some insight into the process of selection for action in infant reaching.

In the present study, therefore, looking and reaching behaviour was measured on the same trials, when infants were presented with pairs of objects of different sizes. Kinematic records of infants' reaches were also collected, to test whether the input of visual information about object size into the control of reaching was reflected in the motor programming of infants' reaches at different ages.

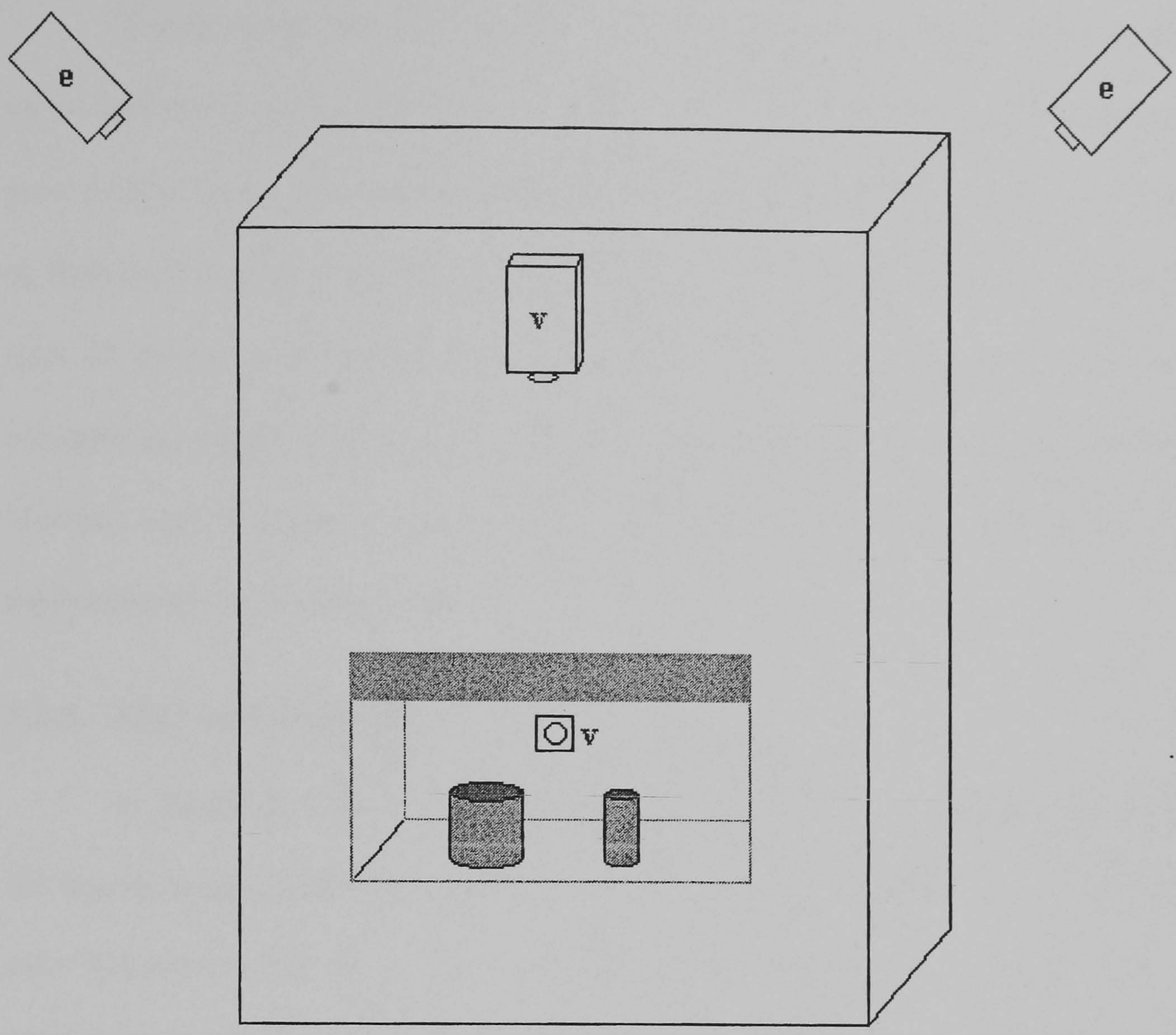
3.2 METHOD

3.2.1. Participants

Participants were 39 infants between the ages of 5 – 15 months old. (16 aged 5-8½ months, 13 aged 8 ½-12 months, 10 aged 12 -15 months).

Figure 3.1 Schematic of experimental apparatus.

V = video camera e = Elite camera



3.2.2. Apparatus

Objects were three red, solid plastic cylinders 6 cm long, of three diameters: ***Small*** (1 cm), ***Medium*** (2.5 cm) and ***Large*** (6 cm). The largest object was too large for the younger infants to grasp easily with one hand. However, some of the infants over 11 months of age were able to pick up this object.

Pairs of objects were presented 12 cm apart in a 'theatre' with a screen that could be raised and lowered using a pulley system. (See Figure. 3.1.) The theatre was

surrounded by grey screens, which created a neutral environment, free from distractions while the infant was presented with the objects.

Video cameras were positioned inside the theatre behind the objects (frontal view) and directly above the infant (saggital view). The camera behind the objects gave a clear record of infants' fixation shifts between the objects, and the moment of first hand contact with either of the objects. The overhead camera enabled the start of the reach to be identified accurately. The signals from the two video records were combined using a Sony video mixer and recorded as one picture on a U-matic tape recorder. A time record, calibrated in 10 msec intervals, was superimposed on the video record.

3.2.3. Elite motion tracking.

A reflective marker was attached to the subject's hand at the first knuckle of the thumb, to enable the hand trajectory to be tracked by the Elite system. Trial and error has shown that this is the best location for a single hand marker in order to minimise lost frames. Markers were attached with double-sided tape to a square of hypoallergenic tape, which was then stuck onto the infant's hand. Markers were also attached to the objects, on the top surface at the circumference.

The Elite record and the timed video record were synchronised, by using the same keypress to start both recordings.

3.2.5. Procedure

Infants sat on the carer's lap, facing the opening of the theatre. Only one hand was used for each trial, the carer gently restraining the non-reaching hand. The height of the carer's chair was adjusted so that infants could reach easily for the objects. The distance from the screen to the infant's chest was about 30 cm. At the start of the

experiment, infants were familiarised with the equipment by hiding a toy behind the screen, raising and lowering the screen a few times, and allowing the infant to reach for the toy when the screen was raised. The objects were then presented in heterogeneous pairs. For each trial, the raising of the screen was the signal to start the video timer and the Elite record. The trial was terminated when the infant first touched or grasped one of the objects. If the infant grasped the object they were allowed to hold it for a few seconds. The screen was then lowered, and a new pair of objects was set in place behind the screen. If after 20 seconds the infant had not made contact with the object, the screen was lowered and another pair was presented. Reaches made on such trials were not scored.

Trials with each hand were performed in separate blocks of 12 trials each, with short breaks after every four trials. Infants were tested in a calm, alert state. If the infant lost interest or became agitated before all the trials were completed, the session was terminated. Infants performed an average of 23.7 trials each. Overall, 470 trials were performed with the right hand, 478 with the left hand.

Some infants spotted the Elite markers on the back of their hands, and tried to take them off or eat them. If the infant's attention could not be distracted from the markers, they were removed and the experiment continued without kinematic acquisition. Some trials were also lost due to occlusion of one or other camera's view of the hand marker during the reach epoch identified from the video record. Kinematic data was included for 27 infants overall (5-8½ month group; n = 10, mean 10.6 trials, range 4 - 18 trials. 8½-12 month group; n = 11, mean 11.7 trials, range 4 - 19 trials. 12-15 month group; n = 6, mean 10.6 trials, range 4 - 19 trials).

The time of occurrence of onset and offset of each fixation upon the objects, the initiation of the reach and the time of contact with the chosen object were coded from the video record of each trial. This record was also used to identify the relevant portion of the ELITE record for kinematic analysis of the reach.

3.2.6. Design

There were 6 possible object pairings, presented in 4 blocks, giving 24 trials overall. Order of presentation was randomised within each block. 12 trials were performed with each hand. Half the infants performed the first 12 trials with their left hand, half with their right hand.

3.2.7. Dependent variables

The video record was used to derive a number of dependent variables for further analysis:

First touch:- the object first touched by the fingers or palm. Touches with the back of the hand were classed as accidental and excluded from the analysis.

First look the object to which a look was first directed after raising the screen.

Fixation duration-: the time spent looking at both objects between first fixation and the start of the reach.

Number of fixations:- the number of fixations on the objects before reach onset.

Look at reach onset:- the object being fixated at the start of the reach.

3.2.8. Data analysis

Wherever data was in the form of proportions, for instance, percentage of first looks to the smallest object in each pair, an arcsine transform was used on the data (Howell, 1992).

The percentage of first looks and first touches to each object was calculated for each subject. ANOVA analysis was used to test for differences in the proportion of reaches to the smaller object in each pair, between pairings and across age groups. As age group boundaries in a continuous sample are inevitably somewhat arbitrary, this analysis was backed up by a regression analysis. The dependent variable was the proportion of responses (first touches) to the smaller object in conditions where the Small or Medium object was paired with the Large (ungraspable) object. The reasoning here was that as infants become progressively more able to use visual information to predict the potential for manipulation of objects, the proportion of reaches to the smaller objects should increase, and these objects should be preferred until infants' hands are large enough to grasp the Large object. A similar analysis was used on looking behaviour. As this analysis does not address the question of which object within each pairing is preferred, one-sample t-tests were used to test whether the proportion of looks or reaches to the smaller object, aggregated across pairings, was significantly different from the chance level of 50%.

3.3 RESULTS

3.3.1. First touch.

Figure 3.2 shows the proportion of reaches to the smaller object of each pair, within each age group. A 3x3 mixed model ANOVA with one within-subjects

factor (pairing) and one between-subjects factor (age group) was used to compare the frequency of reaches to the smaller object of each pair across age groups and pairings. The effect of age group was significant, $F(2,36 = 2.42, p<0.01)$. There was no effect of pairing, and the interaction was not significant. Post-hoc contrasts (Tukeys HSD), revealed that only the difference between means for the 5-8 ½ month group and the 8 ½-12 month group was significant.

A statistical comparison was also made of the number of first reaches to the smaller object of the pair, within each age group. One sample t-tests were used to test the null hypothesis that 50% of touches would be made to the smaller object, aggregated over all pairings. In the 5-8½ month age group there were no significant differences in the number of reaches to the smaller or larger objects. Infants in the 8½ -12 month age group, however, were significantly more likely to touch the smaller object ($t(12 = 2.75, p<0.02)$. Infants over 12 months again showed no preference for smaller objects.

Figure 3.3 is a plot of the percentage of reaches to the smaller object as a function of age in conditions where the Small or Medium object was paired with the Large (ungraspable) object. A linear regression was not significant, $F(1,38) = 3.6; p<0.07$, However, a model including both linear and quadratic terms was significant, $F(2,37) = 5.1 ; p<0.01$, R-sq = 0.22. The F test on the change in R-sq (0.11) between the linear and quadratic model was significant, $F (1,36) = 4.48 ; p<0.04$. This regression analysis confirms that there is a significant change in manual reaching preference as infants get older, with reaches to the smaller objects increasing to a maximum at around 11 months and then decreasing after this age.

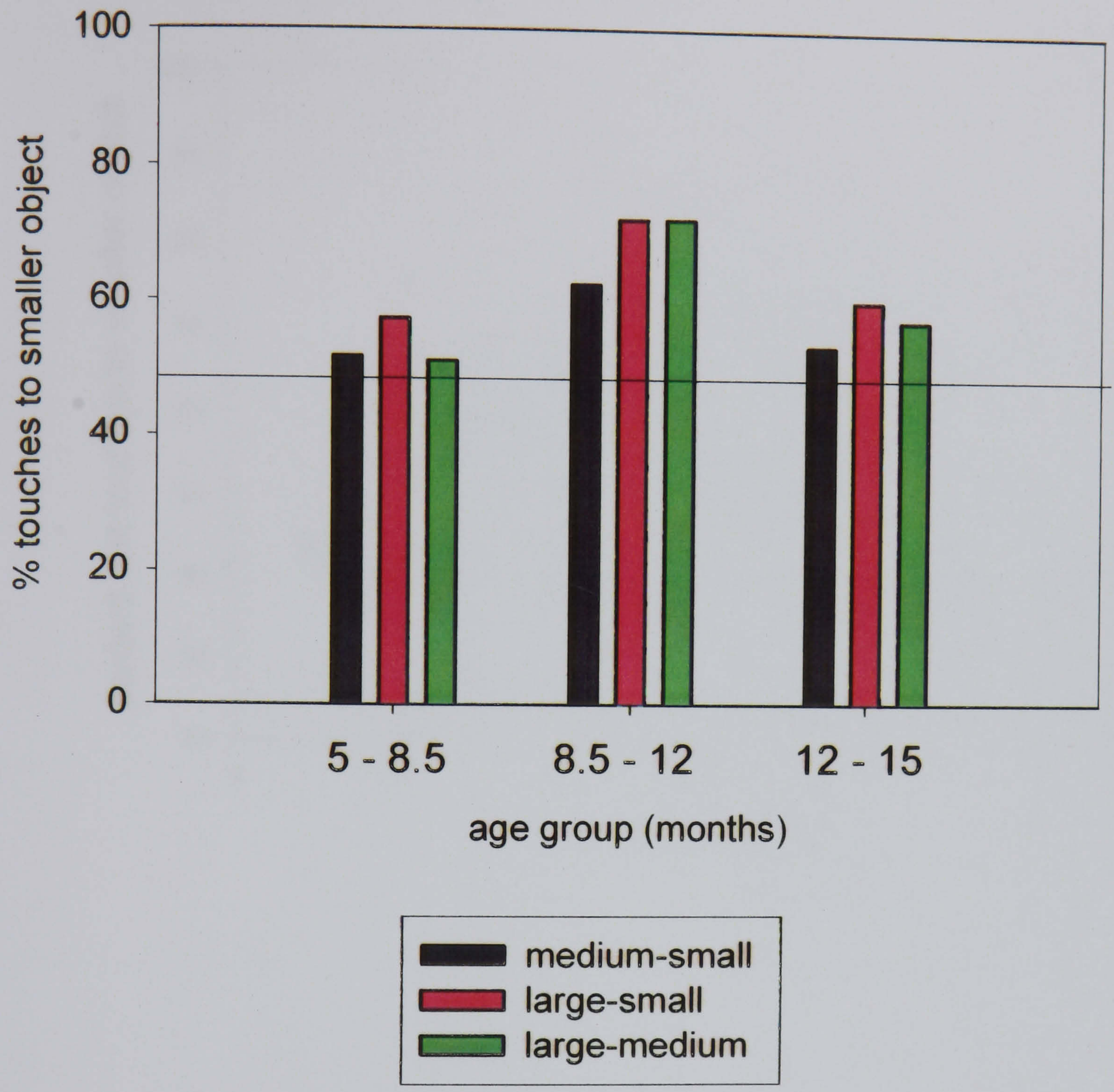


Figure 3.2 Preferential reaching. In the 8.5-12 month age group there is a significant reaching preference for the smaller cylinder of each pair. The preference is not present in children over 1 yr, whose hands are more likely to be large enough to grasp the large cylinder. (Note that 50% is the chance level).

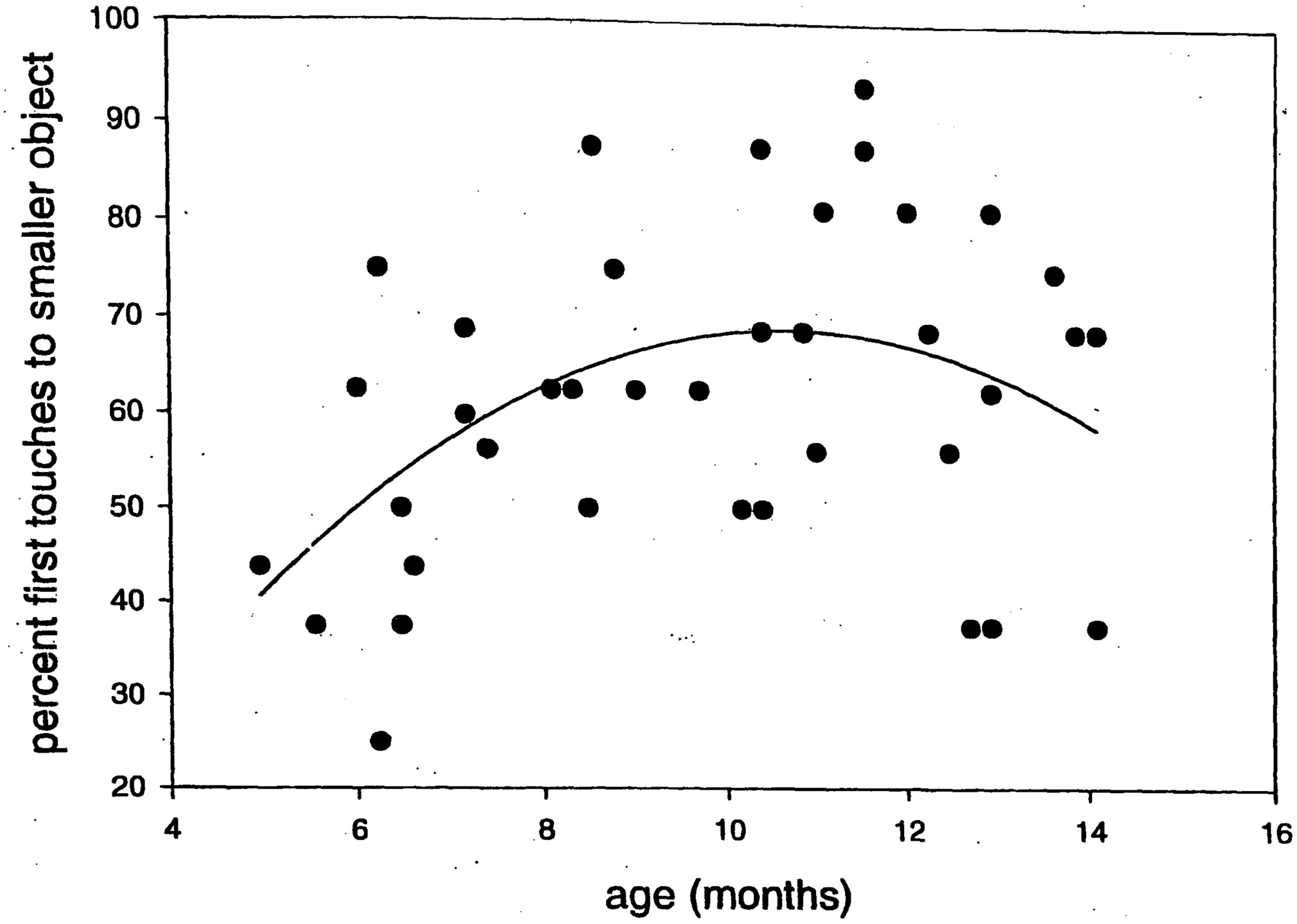


Figure 3.3. Percentage of first touches to the smaller object in conditions where the small or medium object was paired with the large (ungraspable) object, by age of subject. Regression equation is yi = -19.45 + 16.05x - 0.73x2. Quadratic line of best fit is superimposed..

3.3.1.1 Reaches to the Large object

It is possible that object size is less of a constraint upon object choice for infants in the oldest age group because they are able to pick up the large object. To test for this possibility, the proportion of trials in which the infant successfully picked up the large object was recorded. Firstly, the number of infants who were able to pick up the large object on at least one trial varied between age groups (4/16 in the 5–8½ month group, 8/13 in the 8½-12 month group and 9/10 in the 12 – 15 month group). Secondly, the proportion of reaches for the large object which ended in the infant successfully picking up the object varied between age groups (5% in the 5–8½ month group, 29% in the 8½-12 month group and 58% in the 12 – 15 month group). Thus this data suggests that whilst some infants below 12 months were able to pick up the large object, the older infants found it easier to do so.

3.3.1.2 Ipsilateral reaching bias

There was also a strong tendency for first contact to be with the object on the side closest to the reaching hand in all age groups (76% in the 5–8½ month group, 74% in the 8½-12 month group and 73% in the 12 – 15 month group).

It is possible that the lack of a preference for smaller objects observed in the youngest infants could be due to this ipsilateral bias in reaching– if infants reach exclusively for the object on the same side as the reaching hand, they are constrained to select the larger object in 50% of trials. However, a number of factors make this unlikely. Firstly, the level of ipsilateral reaching was similar across age groups. Secondly, there was no correlation between age and the percentage of ipsilateral reaches, even within the youngest age group ($r = -0.06$ ns) or between the percentage of first touches to the smaller object and the percentage of ipsilateral reaches ($r=0.1$ ns). Also, there were infants with very low levels of contralateral reaching (reaching

contralaterally on less than 3 trials) in all three age groups (2 infants in the 5-8 ½ month age group, 3 in the 8 ½ months group, and 2 in the 12 – 15 month group.

The developmental changes in preference for the smaller object were preserved when ipsilateral and contralateral reaches were analysed separately (see Table 3.1).

Table 3 1. Percentage of ipsilateral and contralateral reaches to the smaller object of each pair.

Age group	Percentage of ipsilateral reaches to the smaller object of each pair	Percentage of contralateral reaches to the smaller object of each pair
5 - 8.5	51.55	56.00
8.5 - 12	63.12	86.24
12 - 15	55.83	65.55

3.3.2. First look

3.3.2.1 Object first looked at

Figure 3.4 shows the proportion of first looks to the smaller object of each pair, within each age group. A 3x3 mixed model ANOVA with one within-subjects factor (pairing; LS, LM, MS) and one between-subjects factor (age group; 5-8½, 8½-12 , 12-15 months) was used to compare the frequency of looks to the smaller object of each pair across age groups and pairings. There were no significant main effects or interactions.

A statistical comparison was also made of the number of first looks to the smaller object of the pair, within each age group. One sample t-tests were used to test the null hypothesis that 50% of first looks would be made to the smaller object, aggregated over all pairings. Infants in the 5-8½ month age group, and the 8½-12

Figure 3.4 Preferential looking. Infants of 5-12 months tended to look at the *larger* diameter cylinder first. (Note that 50% is the chance level).

month age group, were significantly more likely to look first at the smaller object (5-8½ month - $t(15) = -2.76$, $p<0.02$; 8½-12 month - $t(12) = -2.26$, $p<0.05$). Infants over 12 months showed no significant preference for smaller objects.

A linear regression was used to model the effect of age on looking behaviour. The predictor variable was age; the dependent variable was the overall proportion for each subject of first looks to the smaller object in conditions where the Small or Medium object was paired with the Large (ungraspable) object. The linear coefficient was positive, ($R = .23$) but was not significantly different from zero.

3.3.2.2 Side of first look

A majority of first looks were to the right, for infants in all age groups. (5-8½ month, 57%; 8½-12 month, 60%; 12-15 month, 56%). A one-sample t-test performed on all subjects' data, using the null hypothesis that 50% of first looks would be to the right, was significant $t(38) = 3.1$; $p<0.004$. This result is an extension of previous findings that there is a rightward bias in preferential looking to computer-rendered 2D representations of the same objects used in this experiment (King, *et al.* 1998).

3.3.3 Fixation duration

The mean time between first fixation and initiation of the reach, broken down into time looking at the objects and time looking away, is presented in Table 3.3 (aggregated over all trials). Fixation duration data was analysed using a mixed design ANOVA with one within-subjects factor, (size of object; small, medium, large) and one between-subjects factor (age group; 5-8½ months, 8½ -12 months, 12 – 17 months). There was no significant difference in the amount of time spent looking at any of the three objects. However, there was a significant difference in

overall inspection time between age groups, $F(2,37)=3.96$, $p < 0.03$. Post-hoc comparisons using Tukey's HSD showed that 8½-12 month old babies spent more time looking at the objects before reaching than infants in the other two age groups.

Table 3.2. Mean time spent looking at the objects, and time spent looking away from the objects, (in seconds), before the initiation of the reach.

Age group	Time looking at objects	Time looking away	Mean total latency
5-8½ months	0.42	0.22	0.64
8 ½-12 months	0.65	0.42	0.75
12-15 months	0.46	0.52	0.49

3.3.3.1 Number of fixations before reach onset.

The next question was whether the increase in inspection time was due to an increase in the duration of individual fixations, or a change in the number of fixations before reach onset. Accordingly, for each infant, the mean fixation length, and the mean number of fixations on the objects before reach onset was calculated, and used a one way ANOVA to test for differences between age groups.

Mean fixation length did not change significantly between age groups, ($F < 1$) but there was a significant difference in the mean number of fixations between age groups ($F(2, 36) = 4.7$, $p<0.02$. Post hoc contrasts (Tukeys HSD) showed that infants in the 8½-12 month age group look back and forth between the objects more frequently than infants in the other two age groups.

3.3.4. Relationship between looking and reaching

One aim of this study was to study possible interactions between different visuomotor sub-systems. In order to test whether initial looking preferences were

influencing reaching behaviour, the relationship was measured between the first look and two other variables; the object being fixated at the start of the reach and the object finally touched.

In a majority of trials the first object looked at was the one being fixated at the onset of the reach. These were termed *look-congruent* trials. Mean percent of look-congruent trials for each age group were: 5-8½ months, 78%; 8½ -12 months, 61%; 12 – 15 months, 68%). One way ANOVA showed a significant difference between groups $F(2,36) = 7.77$ $p<0.002$. Post-hoc contrasts showed that 5-8½ month infants were significantly more likely than the infants in both the other age groups to initiate the reach while fixating the same object they first looked at.

Because infants often looked back and forth between the objects between first look and reach onset, the proportion of trials where the infant reached during the first fixation, i.e. without looking back and forth between the objects was also calculated. Infants in the 5-8 ½ month group were also more likely to reach during the first fixation (percent of reaches made during first fixation: 5-8½ months, 47%; 8½ -12 months, 35%; 12 – 17 months, 37%).

Lastly the proportion of trials in which the object finally touched was the same as the one fixated at the start of the reach was calculated. These were termed reach-congruent trials. Infants in the 5-8 ½ month group were more likely than infants in the other two age groups to change the target of the reach after reach onset (percent of reach-congruent trials for each age group: 5-8½ months, 69%; 8½-12 months, 80%; 12 – 17 months, 77%), although these differences were not statistically significant ($F(2,36)=2.2$, $p = 0.12$)

Taken together these results show that infants in the youngest age group were more likely to reach during the first fixation, without looking back and forth

between the objects, and were more likely to initiate a reach to the object first looked at. There may also be a greater tendency for the youngest infants to start the reach looking at one object, but to finally touch the other object.

3.3.5. Kinematic results

3.3.5.1 Dependent variables

A number of dependent variables were calculated from the kinematic record for each trial. These were *movement duration, maximum resultant speed, number of peaks* in the resultant speed profile, *deceleration time* (time after maximum speed) *and straightness.* The straightness index was calculated by dividing the total distance travelled by the shortest distance from the start point to the end point of the reach; thus a perfectly straight reach would have an index of 1, larger index values indicate increasing deviation from a straight line (Hofsten, 1979). Resultant hand speed was calculated as the magnitude of the velocity vector(the speed of the hand along its direction of movement). Hand speed traces were filtered using a second order, low pass Butterworth filter, cut-off frequency 7hz. Peaks were counted which exceeded 20% of the maximum hand speed recorded during that trial.

Each dependent variable was entered into a 3x2 factorial ANOVA, with age group, object and as independent variables. Means and standard deviations are presented in tables 3.3 to 3.5. Figure 3.5 represents exemplar plots of hand speed for infants at 7, 9 and 12½ months respectively.

3.3.5.2 Movement duration

There were no significant main effects or interactions.

3.3.5.3 Maximum hand speed

The main effect of age group was significant, $F(2,24) = 4.76$, $p < 0.02$. Post-hoc contrasts showed that maximum hand speed was significantly lower in infants in the 8 ½-12 month age group than in the other two age groups. There was no significant effect of object reached for.

Table 3.3 Means (and standard deviations) of kinematic variables, by age group.

	5 – 8½ months (n = 107)		8½ - 12 months (n =129)		12 – 15 months (n = 64)	
Dependent variable						
Duration (ms)	**980.91**	(620.62)	**1340.71**	(950.71)	**1060.43**	(572.2)
Peak hand speed (mm/s)	**432.40**	(220.65)	**301.60**	(142.34)	**382.09**	(162.24)
No.of peaks	**1.74**	(1.03)	**2.17**	(1.45)	**1.88**	(1.16)
Straightness index	**1.43**	(0.82)	**1.37**	(0.43)	**1.41**	(0.57)
Deceleration time (ms)	**590.55**	(510.09)	**910.39**	(910.04)	**703.75**	(467.63)

Table 3.4 Means (and standard deviations) of kinematic variables, by object reached for.

	Small (n=121)		Medium (n=117)		Large (n=62)	
Dependent variable						
Duration (ms)	**1280.49**	(969.98)	**1059.60**	(617.60)	**1101.61**	(669.90)
Peak hand speed (mm/s)	**360.56**	(175.07)	**369.93**	(207.91)	**367.90**	(168.59)
No.of peaks	**1.99**	(1.45)	**1.92**	(1.09)	**2.01**	(1.24)
Straightness index	**1.42**	(0.63)	**1.35**	(0.51)	**1.48**	(0.81)
Deceleration time (ms)	**876.60**	(863.68)	**665.80**	(541.14)	**691.10**	(667.71)

Table 3.5. Means (and standard deviations) of kinematic variables, by side of reach.

	Ipsilateral (n=224)		Contralateral (n=76)	
Dependent variable				
Duration (ms)	**1105.54**	(744.47)	**1310.76**	(905.54)
Peak hand speed (mm/s)	**353.29**	(181.63)	**401.22**	(198.31)
No.of peaks	**1.95**	(1.28)	**2.00**	(1.30)
Straightness index	**1.40**	(0.54)	**1.43**	(0.84)
Deceleration time (ms)	**720.40**	(657.83)	**840.40**	(866.73)

3.3.5.4 Number of peaks

There were no significant main effects or interactions.

3.3.5.4 Straightness

There were no significant main effects or interactions.

3.3.5.5 Deceleration time

The main effect of age group was significant, $F(2,24) = 4.5$, $p<0.02$. No other main effects or interactions were significant. Post-hoc contrasts (Tukey's HSD) showed that deceleration time was significantly longer in the 8 ½-12 month infants than in the other two age groups.

Differences between ipsilateral and contralateral reaches were analysed using paired t-tests. Maximum hand speed was higher for contralateral than for ipsilateral reaches, $t(26)=2.51$, $p<0.02$. None of the other measures showed significant differences between ipsilateral and contralateral reaches.

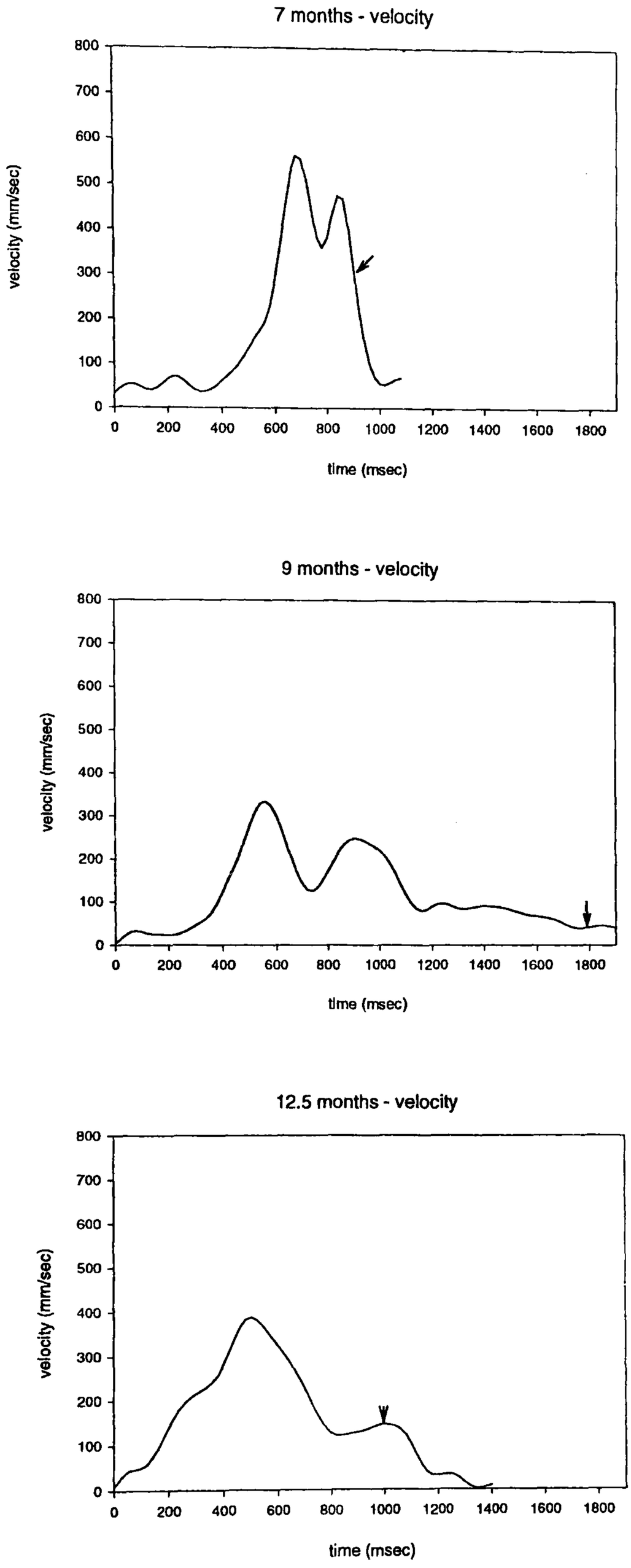


Figure 3.5 Exemplar hand speed plots from infants at 7 months, 9 months and 12.5 months. The arrow indicates time of contact with the object. Infants in all age groups showed multi-segment reaches. However, these were more common in the 8 ½-12 month age range.

3.3.5.6 Summary of kinematic results.

Reaches made by infants in the 8½-12 month age group showed more time spent in deceleration and lower maximum hand speed than those made by infants in the other two age groups. (This pattern of results was present for ipsilateral and contralateral reaches, when they were analysed separately. It is therefore unlikely that differences between age groups in maximum hand speed are due to small differences in the proportions of ipsilateral and contralateral reaches across age groups). There were no significant differences between reaches to different objects in any of the kinematic variables measured. Ipsilateral reaches showed lower maximum hand speed than contralateral reaches..

3.4 DISCUSSION

This study found that that systems controlling looking and reaching are preferentially activated by different object attributes in infants between 8½-12 months. The prediction that there would be an age-related increase in reaching to graspable objects was confirmed. This developing sensitivity to the affordances of objects in infants over 8 ½ months implies either that ventral stream recognition mechanisms are attuned to visual inputs which signal the graspability of an object, and can communicate this information to the dorsal stream, or that feedback from implicit object processing in the dorsal stream is providing information about an object's potential for manipulation, without the need to access stored representations. (Rizzolati, 2000).

However, this development in the visual control of reaching involves a degree of decoupling between the target selection mechanisms for reaching and looking. Up to 12 months, the larger object remains the preferred target for looking, suggesting that this

behaviour is driven by mechanisms that respond to general visual salience independent of the object's potential for manual action.

Whilst the current results leave open the question of whether the ventral and dorsal streams are functionally differentiated at the onset of reaching, they do provide us with an insight into the development of selection for action processes in infants. In particular, a more detailed investigation of the pattern of looks and reaches in each trial gave rise to a number of unexpected results. Firstly, infants in the youngest age group, who showed no specific reaching preference, were more likely to reach for the first object fixated in any trial. Secondly, those infants who preferred to reach for graspable objects also looked back and forth between the objects more. This implies that in order to visually scan a scene and select a suitable target for action infants must first inhibit a coupled look-reach response.

3.4.1. Preferential reaching

Infants of all ages in this experiment reached almost compulsively for objects presented to them. However, while 5–8½ month infants show no preference when reaching to objects of different sizes, 8½ -12 month infants show a strong preference for smaller objects (see Fig. 3.2). This effect cannot be explained by a change in the proportion of ipsilateral reaches between age groups. The proportion of ipsilateral reaches was almost constant across age groups, and there was a similar number of infants who displayed very high levels of ipsilateral reaching in all three age groups.

It is likely, therefore, that this effect indicates a developing ability to use visual information to predict which objects will be easy to manipulate. The observed effect appeared weaker in infants over 12 months, presumably because they were more likely to be able to pick up the Large object. One factor underlying the increase in reaches to

smaller objects observed after 8½ months may be the maturation of the neural pathways involved in prehension, especially the improved control of fine finger movements associated with myelinisation of the corticomotoneuronal tract, (see Armand *et al.* 1996 for a review). It is at this stage that co-ordination between the proximal and distal components of prehension is first being achieved, with accompanying advances in visuo-motor and visuo-cognitive abilities. There may be a process of reciprocal influence, with increasing motor competence giving rise to an increase in the attractiveness to infants of objects that are easy to manipulate. Current models of adult function suggest that this process requires an interaction between identity-selection processes in the ventral stream and pre-frontal cortex with modules in the dorsal stream which transform visual information about objects into object-oriented movement. Previous studies indicate that infants use a combination of immediate visual input and visual memory to guide their actions. Thus, Granrud *et al.* 1985 have shown that 7 month infants use memory of previous experience of objects in making judgements of apparent distance. Clifton *et al.* (1991) have also reported that reaching in the dark by 6½ month infants is guided by memory of previously seen objects. The infants who were consistently selecting smaller objects in this experiment may have been using their memory of the objects gained during the experiment, or representations of similar objects from outside the experimental context. It is also possible that feedback mechanisms within the dorsal stream may give an 'online' signal when an object is too large for the hand. This may explain those instances where the infants started the reach looking at one object, but finally touched the other object. Whilst the processes underlying object recognition and object-oriented action are thought to be organised in a modular fashion in adults (Milner and Goodale, 1995) it is not known whether the development of object processing in the visual system reflects pre-specified modules

"coming online", or whether the modularisation of visuomotor pathways is an outcome of developmental processes.

3.4.2. Kinematic evidence

The kinematic evidence from this study suggests that there is an important transition period in motor competence in the last part of the first year of life. When one looks at the kinematics of the reach in 8½-12 month infants, maximum hand speed is lower, and the deceleration time is longer (see table 3.5). The higher maximum hand speed and shorter deceleration times in the 5-8½ month infants' reaches are consistent with the idea that early reaches are less controlled, and less adapted to the properties of the target object. This is consistent with evidence from other researchers (e.g. Mathew and Cook, 1990; Konczak and Dichgans, 1997; or a review from the dynamic systems perspective of what variables an infant learns to control in order to execute a successful reach to a desired object, see Thelen, 1998).). Also, Clifton *et al.* (1994) have observed that 6 month old infants show higher peak velocity and shorter duration when they reached in the dark for objects whose position was defined by a sound, than when they reached in the light. However, when reaching for a glowing object in the dark, without visual feedback about limb position, there were no significant differences in peak velocity and duration. Thus it seems that visual information about limb position is less important in planning the reach at this age than visual feedback about the position of the target. It is therefore reasonable to suppose that our 8½-12 month group were reaching more slowly than the youngest infants because they are making greater use of visual information about the target object.

Decreased maximum hand speed and increased deceleration time in the 8½ - 12 month age group suggest that the early stages of object-oriented action requires a slowing down of the reach, and an extended 'homing-in' phase. It has been suggested that the deceleration phase in adult prehension is the portion of the reach where visual

feedback is used to make adjustments in trajectory before final contact with the object (Jeannerod, 1988 p 66).

3.4.3. Preferential looking

In previous work in this laboratory were shown 2D computer renditions of the same 3D stimuli in two conditions: with either the inner edges of the objects or the centres of the objects equidistant from an initial central fixation point (in the latter condition, therefore, the inner edge of the larger diameter object would be closer to the fixation point). Infants between 5 and 12 months were found to look first to the largest object in a pair, in the condition where the edge of the larger object was nearer to the central fixation point. (King *et al.* 1998). Where the distance of the object's inner edge from the fixation point was equalised, younger infants showed a preference for the Medium cylinder in LM and ML pairs, whereas older subjects tended to look first at the Large cylinder. However, this was when looking at two-dimensional displays displayed on a computer screen, with a fixation stimulus displayed between each presentation of the stimuli. In the present study, during a more naturalistic reaching task to 3D objects, the preference for looking at the larger object of the pair is statistically significant in infants aged between 5 and 12 months (Fig. 3.4). Taken together, these results suggest that visual orienting in infants up to 12 months seems to be drawn to the larger object either because its edge is nearer to a fixation point, or simply because it represents a larger patch of contrast and colour in the visual field when the screen is first raised. The evidence from the present study suggests that even during a reaching task, it is these features rather than graspability which are the most salient for the visual orienting system in the first year of life.

Infants in this study and that of King *et al.* (1998) showed a significant rightward bias in the direction of the first look. Cohen (1972) reports that 4-month old infants look longer and turn more quickly towards stimuli presented on the right than on the left. Right biases have also been reported in head position preference in newborns (Ronnquist and Hopkins, 1998), and also in the ease with which head turning can be conditioned in both newborns and older infants (Siqueland and Lipsitt, 1966) (Siqueland,1964). It has been proposed that asymmetries in the head position of newborns are caused by differential stimulation of the vestibular system during gestation (Previc, 1991). This study demonstrates that a bias is still present in infants up to 15 months in the frequency of first looks to the right. It is possible that the asymmetries observed in newborns set up an orienting bias for the right side of peripersonal space in the first months of life. The bias is not present, however, in the amount of time spent looking at the objects before reaching. This suggests that this bias is present in the visual orienting system, but does not necessarily bias the total information intake during the preparation of the reach.

3.4.4. Time spent looking at the objects before reaching

Fixation duration measures indicate that the time spent looking at the objects before reaching increases after 8½ months, but decreases again in infants over 12 months. Analysis of the number of fixations made in each trial indicates that these changes in overall looking time are due to changes in the number of times infants look back and forth between objects rather than changes in the duration of individual fixations. Whilst both the youngest and the oldest infants look back and forth between the objects less, the reasons for this are probably different in the two age groups. Younger infants seem to reach quite reflexively, frequently to the first object they fixate. Older infants are more practised in analysing the relevant

features of objects in order to choose which objects will be most interesting to interact with. The increased number of fixations observed in the 8½-12 month infants may reflect the extra time taken to process object attributes before reaching, when this skill is first being acquired. A delay in reaching may also be caused by the need to inhibit an immediate reaching response to the first object they look at (see below), or by the heavy processing demands of planning a reach.

3.4.5. Congruence between reaching and looking

5–8½ month infants were more likely to initiate the reach whilst fixating the first object looked at. There is a significant decrease in this tendency in infants over 8½ months. One of the factors underlying the development of the ability to select and reach for a desired target may be the uncoupling of this early linkage between reaching and visual orienting. A number of other researchers have postulated such a link. Hofsten (1991) reports that in neonates, forward extensions of the arm made when an object was fixated showed a smaller deviation from target direction than those movements initiated without fixation of the target. Hofsten contends that this early linking of looking and reaching is an attentional rather than manipulative response. "When the neonate looks at and reaches for an object, both the reaching and the looking are parts of the same orienting response toward the object....The convergent attitude of the eye and hand toward the object constitutes a favourable foundation for the subsequent development of eye-hand co-ordination' (Hofsten 1989).

Gauthier *et al.* (1988) also proposed that eye and hand movements are controlled by separate sensorimotor systems, which are initially tightly coupled. In their view, versatility and skill in movement is based upon the development of a

mechanism that is able to override this coupling and co-ordinate the interaction between the two systems. Whilst a linkage between eye and arm movements may be initially functional, in that it will tend to get the arm near to an interesting object, true flexibility in reaching requires the ability break this link. It is likely that both the visual orienting and the reaching behaviour observed in this experiment involve closely linked cell assemblies in neural circuits controlling prehension and oculomotor activity. Snyder *et al.* (1996) for instance, reported that some reach-specific neurons in the intraparietal sulcus of the monkey are active before saccades, and that some saccade-specific neurons are active before a reach, which may reflect the fact these movements are often made concurrently. This experiment provides evidence for an emerging ability to selectively inhibit these anatomically and functionally linked behaviours.

3.4.6 Contralateral reaching

One question that has been raised but not answered in the literature on infant reaching is the extent to which infants are capable of making reaches across the midline. Bruner (1969) proposed that there was a 'midline barrier', based upon his observations that infants rarely reached across the midline. However, Provine and Westerman (1979) found that all infants older than 20 weeks in their study could successfully contact single objects placed in contralateral space. Butterworth *et al.* (1997) report that infants did reach across the midline to single objects of various sizes, and that 30/37 of the contralateral reaches observed ended in a precision grip. Bishop (1990) reports that young infants, like split brain patients, tended to reach for objects with the hand ipsilateral to the desired object. She proposes that maturation of the corpus callosum may enable infants to inhibit the tendency to make symmetrical bimanual movements. On this view, reaching to an object across the midline first requires the inhibition of a

reach with the ipsilateral hand, followed by programming of a reach with the contralateral hand. Thus there is an extra 'cost' in contralateral reaching, in terms of an extra process of inhibition (see also Jeannerod, 1988). In addition, there may be biomechanical reasons why contralateral reaches are more difficult. In adults, reaching movements directed across the midline are slower and less accurate than ipsilateral reaches, (Fisk and Goodale, 1985; Jeannerod,1988; Carey *et al.* 1996). This experiment showed no increase in the overall proportion of contralateral reaches between 5 and 17 months. Thus, these data provide no evidence for a developing ability to reach across the midline.

3.4.7. Conclusion

The combination of preferential reaching, preferential looking and kinematic measures used in this study provide converging evidence of an important transition period in visuomotor competence between the ages of 8½ -12 months. The development of the ability to use visual information to predict the graspability of objects is reflected in the increase in frequency of reaches to graspable objects, and in the increase in the time spent inspecting the objects before reaching. There are concurrent changes in the kinematics of the reach; infants at this age exhibit slower reaches, with an extended 'homing-in' phase as they approach the object to be grasped. Preferential looking measures showed that as infants get older, visual orienting to objects in personal space becomes less dependent on the visual salience of the object. Looking and reaching preferences diverge during the development of reaching. This divergence may reflect dissociation during development of visual processing streams subserving object-related action from those related to visual orienting. Lastly, there is evidence that in early life looking and reaching may be yoked together in the form of a general orienting response.

The maturation of the ability to select and reach for an object may depend upon the selective inhibition of these closely coupled behaviours.

3.5 EXPERIMENT 2: PREFERENTIAL REACHING WITH FREE CHOICE OF HAND TO OBJECTS OF DIFFERENT SIZES.

Infants were restricted to reaching with one hand in Experiment 1. This forced-choice design was a useful way of ensuring an unequivocal choice of object in each trial. However, the fact remains that infants are not generally restricted in their choice of hand when reaching for objects around them. This may mean that the effects observed do not generalise well to more natural reaching situations. Also, whilst infants adapted well to having one hand restrained during the first experiment, it is possible that this constraint restricted flexibility in movement, particularly to objects placed on the opposite side to the reaching hand. This reluctance to reach across the midline may have reduced the effect of object size in the first experiment. To address these questions, another experiment was carried out to test infants' reaching preferences under more naturalistic conditions, when they are presented with a choice of objects of different sizes, and are allowed to reach with either or both hands. Infants were again presented with a pair of objects - a cylinder small enough to grasp with one hand, paired with a large cylinder which would require two hands to pick up. The aims of this experiment were to ascertain whether infants do in fact choose to reach with two hands when given the opportunity, and if so, whether bimanual reaches are made more frequently to the larger object than unimanual reaches.

3.6 METHOD

3.6.1. Subjects

Subjects were 16 infants between 4 months and 12 months. 2 infants (aged 5 months and 8 months) reached for both objects with both hands on nearly every trial. Results from these infants are not included in the analysis.

3.6.2. Apparatus

Two of the same red plastic cylinders used in the first study were used in this experiment (the Large, 6 cm diameter, and Small, 1 cm diameter cylinders).

3.6.3. Procedure

The procedure for this experiment was the same as that for experiment 1, except that infants were not restricted to using one hand to grasp the objects. Each pairing (LS or SL) was presented 12 times, with order of presentation randomised. The direction of the first look and the object first touched were observed.

3.7 RESULTS

305 trials were analysed. Infants performed an average of 22 trials each. (The youngest infant only reached on 11 trials before becoming fussy).

<u>Definition of bimanual reaches</u>

The aim of this study was to determine how infants use visual information when specifying a reach. Reaches where the second hand was recruited after the first hand made contact with the object were therefore classed as one-handed..

Bimanual reaches were defined as reaches where both hands were extended over the threshold of the theatre, and where movement of the second hand started before the

first hand contacted the object. 46/305 reaches (15%) were classed as bimanual. All infants made at least one bimanual reach (minimum 1, maximum 8, mean per infant 3.9 bimanual reaches)

These reaches were broken down as follows:

- 26 reaches where both hands touched the object nearly simultaneously.

- 3 reaches where both hands crossed the theatre threshold, but only one hand touched an object.

- 1 reaches where both hands contacted the object, but one hand touched the object before the other.

- 16 reaches where both hands touched both objects.

3.7.1. First touch: unimanual reaches

18.5% of unimanual reaches crossed the midline, this proportion was similar across age groups (4 - 8½ months, 19%; 8-12 months, 18%).

Figure 3.5 shows the proportion of first touches to the small object for each subject, plotted as a function of age, when infants were reaching with one hand. When infants were divided into two age groups with 8 ½ months as the cut point, there was no statistical difference between the proportion of first reaches to the small object in the two groups (infants under 8 ½ months –58%, infants over 8 ½ months - 55%,. However, it is apparent that there is a group of infants between 7 and 10 months who show a strong preference for reaching to the small object.

A linear regression, predicting the proportion of first touches to the small object from the age of the infant, was not significant, $F(1,12) = 0.76$. However, a model including both linear and quadratic terms was significant, $F(2,37) = 5.1$; $p<0.03$, R-sq = 0.47. The F test on the change in R-sq (0.4) between the linear and

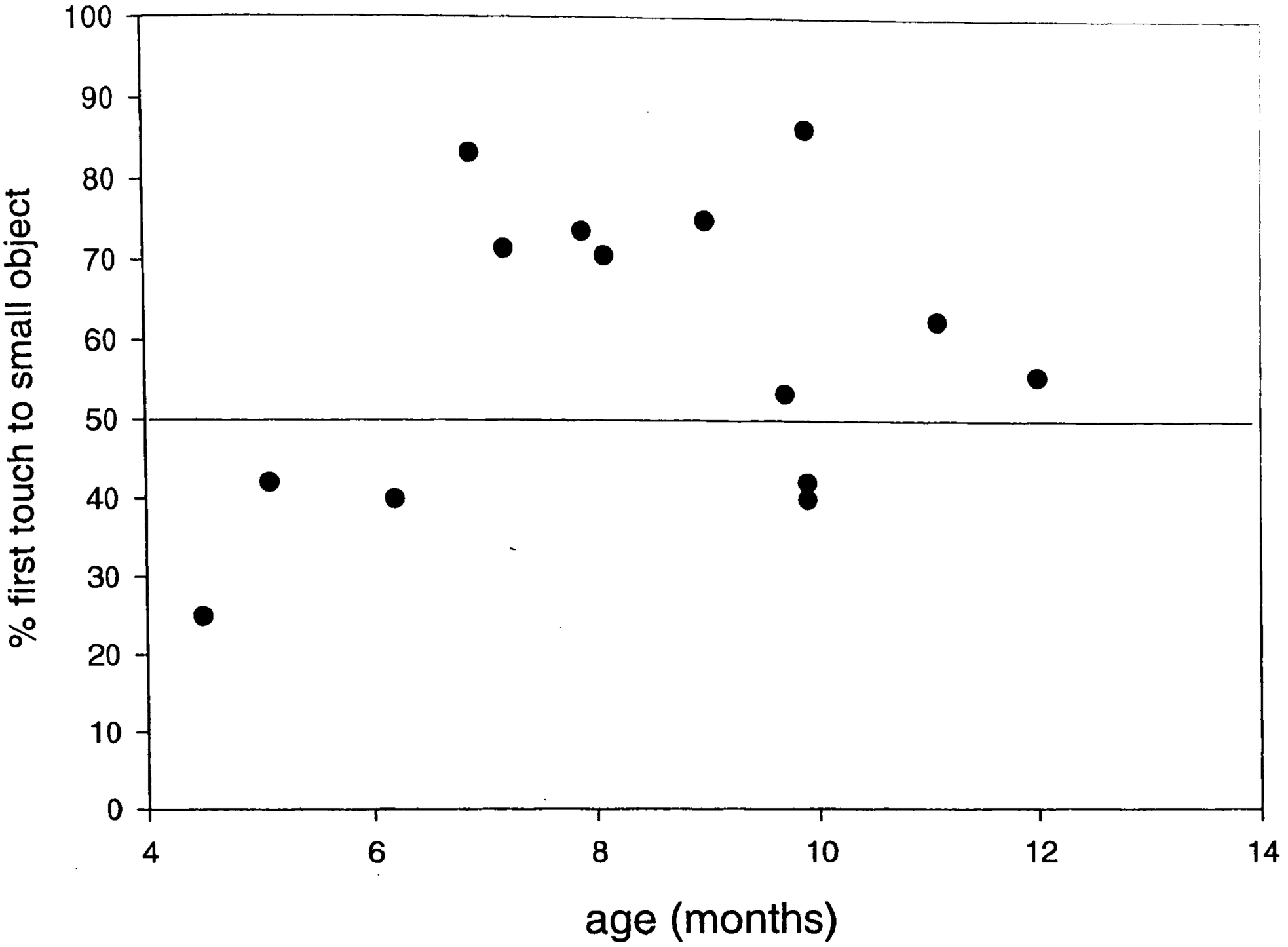


Figure 3.5 The proportion of first touches to the small object for each subject, plotted as a function of age, when infants were reaching with one hand.

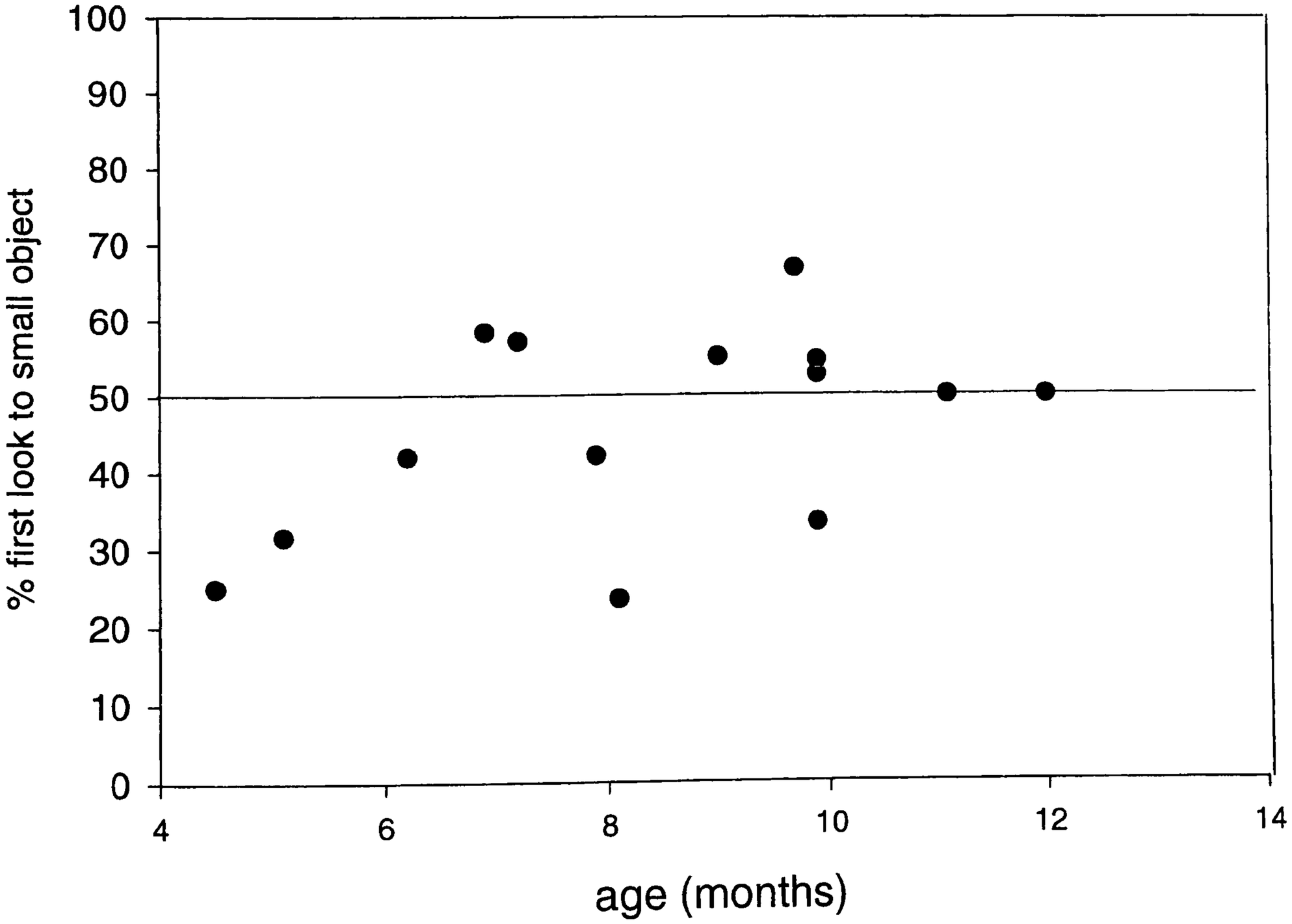


Figure 3.6 Proportion of first looks to the small object, plotted as a function of age.

quadratic model was significant, $F(1,11) = 8.86$; $p<0.03$. This regression analysis confirms that there is a significant change in manual reaching preference as infants get older, with reaches to the smaller objects increasing to a maximum at around 8.7 months and then decreasing after this age.

The data from this experiment have the same pattern as in experiment 1 – in that reaches to the small object increase with age, and then decline. However, it is possible that the age at which a maximum of reaches to the small object is observed is lower in this experiment than in experiment 1 – from inspection of figure 3.5 this point seems to be at about 9 months, compared to 11 months in experiment 1.

3.7.2. First touch: Bimanual reaches

When reaching with two hands, 16/46 of reaches were made with both hands to both objects (5 in the younger age group, 11 in the older age group), and so an object preference could not be coded. Of bimanual reaches which were directed to one object only, 15/29 (52%) of reaches were to the small object. (4 ½ -8½ months, 13/21 (62%) to the small object; 8½-12 months, 2/8 (29%) to the small object).

3.7.3. First look

Figure 3.6 shows the proportion of first looks to the small object for each subject, plotted as a function of age.

It can be seen that infants under 8 ½ months were less likely to look first at the small object, (and so were more likely to look first at the large object). When broken down by age group, 60% of first looks were to the large object in the infants under 8 ½ months, whereas 48% of first looks were to the large object in infants over 8 ½ months. When the proportion of first looks to the small object was compared between age groups, this difference approached statistical significance, $t(12) = 1.9$, $p<0.08$.

3.8 DISCUSSION

This experiment shows that when infants are given a free choice of hand, and a choice of objects, the majority (85 per cent) of reaches were made with one hand. There was also a preference for reaching to the smaller object in a group of infants between 7 and 10 months. The developmental profile of one-handed reaching preferences was therefore similar to that observed in experiment 1, except that the point of maximum preference for small object was at an earlier age –about 9 months instead of 11 months. Two factors could have contributed to this age shift. Firstly, the free choice of hand given in this experiment may have allowed younger infants to display a stronger preference for smaller objects than in experiment 1. Thus, restricting infants to one handed reaching, coupled with the reluctance of infants to reach across the midline, may have restricted younger infants ability to reach for the small object on some trials. Secondly, only the two objects with the largest difference in diameters were used in this experiment. This means that the visual discrimination between graspable and ungraspable objects may have been consistently easier to make than in experiment 1, because of the large difference between the objects. In addition, there was only one discrimination of object size to make, as opposed to 3 possible discriminations in experiment 1 (LS, LM, MS), which may have made the discrimination of graspability easier for younger infants.

Because infants in the first experiment were restricted to reaching with one hand, the reaching preference for smaller objects was interpreted as an emerging ability to use visual information to predict which object is too big for the available hand to grasp. Since, in the present experiment, the infant was allowed to use either or both hands to grasp the objects, both objects were in principle 'graspable'. Given reports in the literature that infants of this age will reach readily with two hands when a single,

larger object is presented to them, (Newell *et al.* 1989) it is unlikely that those infants in this study who showed a preference for the small object were doing so because they had a strong bias towards one-handed reaching. It is more likely that in the course of development, infants simply come to prefer reaching for smaller, more 'handy' objects.

Interestingly, the recruitment of two hands to the reach was not more likely when infants were reaching for the large object. This result is in contrast to that of Newell *et al.* (1989), who have shown that when a single object is presented to infants between 4 and 8 months, they will switch to two-handed reaching when larger objects are presented to them. (However, only 8 month old infants were able to use visual information to choose an appropriate grip before object contact). The difference may arise from differences between the objects used The smallest object used by Newell *et al.* (1989) was a 2.5cm. cube, which is more stable than the cylinder used in this experiment and unlikely to be knocked over when the infant tries to grasp it. Indeed, from observation of the infants performing the current experiment, it seemed that infants were as likely to use a the second hand to provide back up in the tricky operation of grasping the small object, as to enable the large object to be grasped.

Infants again showed a strong bias for ipsilateral reaching. Thus while Provine and Westerman (1979) have demonstrated that infants over 20 weeks are able to reach across the midline if a single object is presented in contralateral space, the results of these experiments show that this is not a preferred option for infants in the first year of life. As Bishop (1990) speculates, contralateral reaching may remain relatively infrequent until a clear hand preference is established, which may not take place until around 3 years of age (Hildreth, 1949).

As in experiment 1, younger infants tended to look first at the Large object. This supports the proposal that visual orientation mechanisms are biased towards the larger object in the visual field in infants under 8 ½ months.

4 Infants reaching and looking preferences to objects varying in size and visual pattern

4.1 EXPERIMENT 3: INTRODUCTION

As discussed in chapter 3, the experimental design used here presents the infants with what Allport (1987) has called a selection for action problem. All animals are constantly required to select appropriate targets for action from complex visual scenes, taking into account their ongoing goals and their bodily capabilities. Meegan and Tipper (1999), in discussing the selection for action problem, propose that all objects in the visual array are processed as potential targets for action, and that processing takes place in parallel in dorsal action pathways and ventral identification pathways. However, they propose that, as processing in the ventral stream is slower than that in dorsal stream (Schmolesky *et al.* 1998), as is the use of ventral stream information in the control of action (Pisella *et al.* 1998), identity selection processes may not always have time to fully inhibit the preparation of actions to inappropriate objects. In adult experiments, this effect is manifested in subtle perturbations of saccades or reaches to objects in the presence of distractors (Castiello, 1996; Meegan and Tipper, 1999).

Infants face the same problems as adults as they explore the world around them. In choosing whether to reach for an object or just to look at it, they need to identify appropriate targets and also inhibit potential reaches to objects which are not in range, or impossible to pick up. However the processes underlying this ability may be still be developing in infants, either, because the various action and identification pathways

may not yet be fully differentiated in the developing brain or because communication between them is not yet fully established.

In Meegan and Tipper's model, the choice of whether to look at or reach for an object would depend upon different levels of inhibition in saccade or reach pathways, depending upon the properties of the object. Therefore, increasing the visual salience of an object which is too large to grasp should increase the likelihood of a saccade towards that object, but reaches to that object should still be inhibited.

The age-related increase in reaches to graspable objects seen in the first experiment indicates that after 8 ½ months, most infants are able to use visual information to predict which objects will be easy to manipulate. In addition, the mechanisms underlying visual orientation and reaching seem to be independent at this age, with the majority of first looks being to the larger object, but the majority of reaches being made to the small object. However, if selection for action mechanisms are not fully developed, it may be possible to increase the likelihood of a reach towards a non-graspable object by increasing its visual salience. This question was addressed by comparing the frequency of reaches and looks to a small graspable object when it was paired with either a large plain object, as in experiment 2 or with a more visually interesting large object, with a schematic face printed on it.

4.2 METHOD

4.2.1. Design

There were 4 possible object pairings, presented in 6 randomised blocks, giving 24 trials overall.

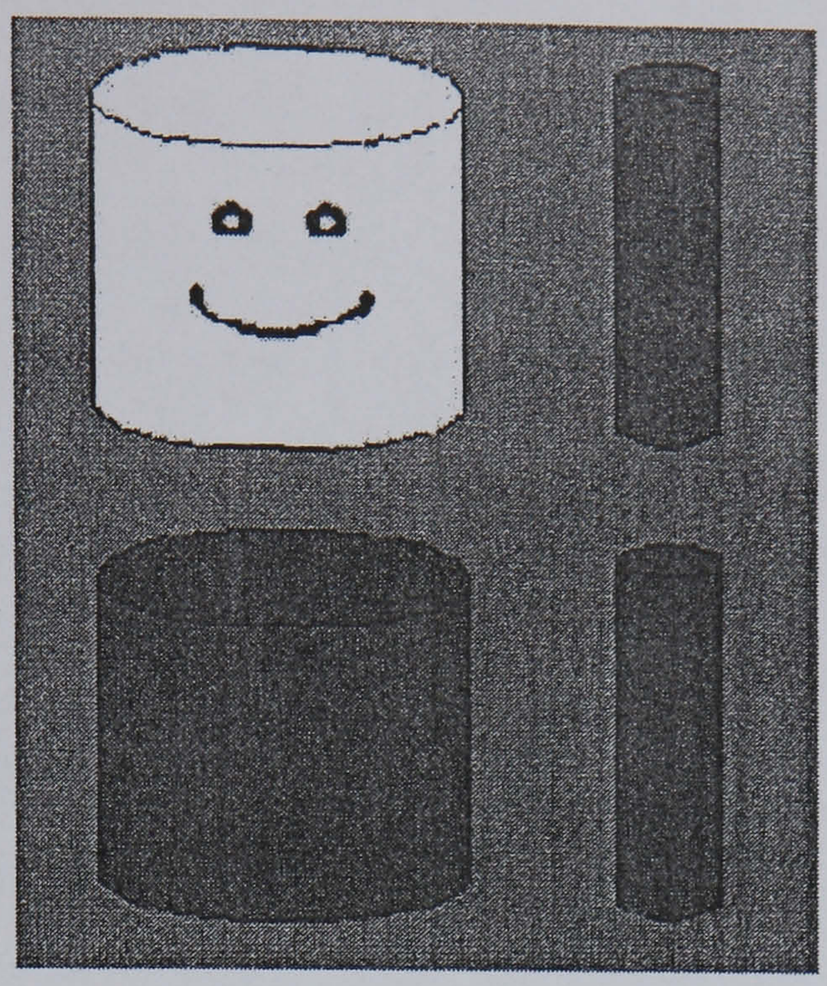


Figure 4.1 Objects used in experiment 3

4.2.2. Participants

Participants were 24 infants between the ages of 5½ –12 months old. (12 aged 5½ -8 ½ months, 12 aged 8 ½-12 months). 1 infant reached for both objects with both hands on every trial. Results from this infant are not included.

4 infants were also studied longitudinally between the ages of 5 and 12 months.

4.2.3. Apparatus

Objects were three solid plastic cylinders 6 cm long; of two diameters; ***Small*** (1cm), or ***Large*** (6 cm). For this experiment, the large object was either plain, or had a schematic face drawn on it (see Fig. 4.1)

4.2.4. Procedure

The procedure for this experiment was the same as that for experiment 2. On each trial infants were presented with a pair of objects - a small 'graspable' cylinder paired with a cylinder too large for the child to grasp. The large object was either plain, or had a

schematic face drawn on it. Twelve presentations were made of the small object paired with the large plain object, (**SL** pairing) randomly interleaved with 12 presentations of the small object paired with the face object (**SF** pairing). The direction of the first look and the object first touched were observed.

4.3 RESULTS (CROSS-SECTIONAL STUDY)

4.3.1. Dependent variables

Manual reaching preference (the object first touched. Touches with the back of the hand were classed as accidental and excluded from the analysis.)

Visual preference (the direction of first look)

4.3.2. Data analysis

Infants performed an average of 21.5 trials each. Data loss was due to some infants becoming uninterested at the end of the experiment (37 trials), accidental touches of the objects (10 trials), or infants occasionally reaching for both objects with both hands (10 trials (this does not include the infant whose data was excluded because he reached for both objects with both hands on every trial); or procedural error (3 trials)

Of the 516 trials analysed, 460 trials (89%) were classed as one-handed reaches.

4.3.3. Manual reaching preference (One-handed reaches)

23% of one handed reaches were to the object contralateral to the reaching hand. This proportion was the same in both age groups. This is very similar to the proportion of contralateral reaches seen in experiment 1.

Figure 4.2 is a plot of the percentage of reaches to the Small object (combined across both object pairings), as a function of the age of the subject. A regression testing

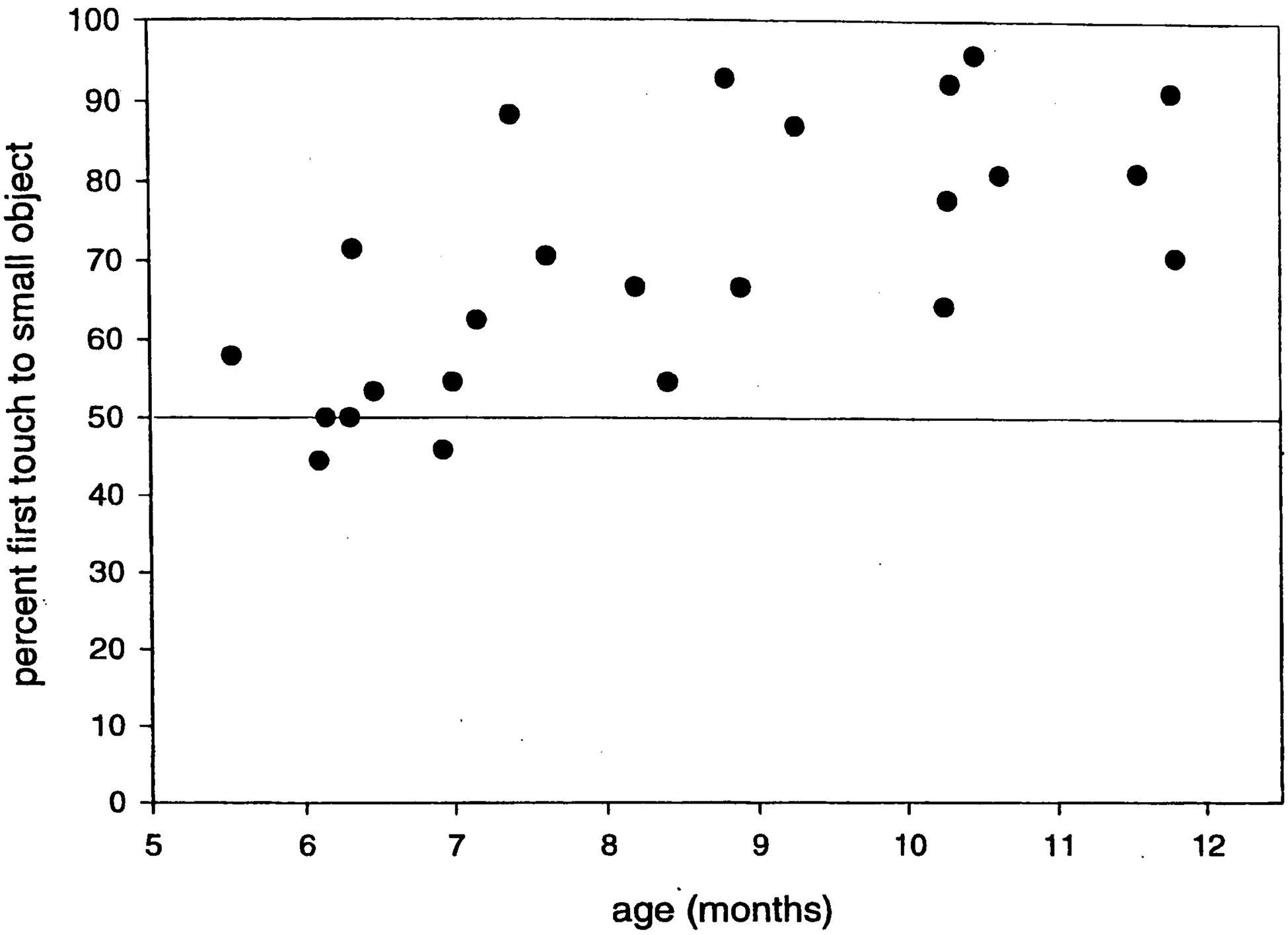


Figure 4.2 Unimanual reaches: Percentage first touches to small object, by age of infant.

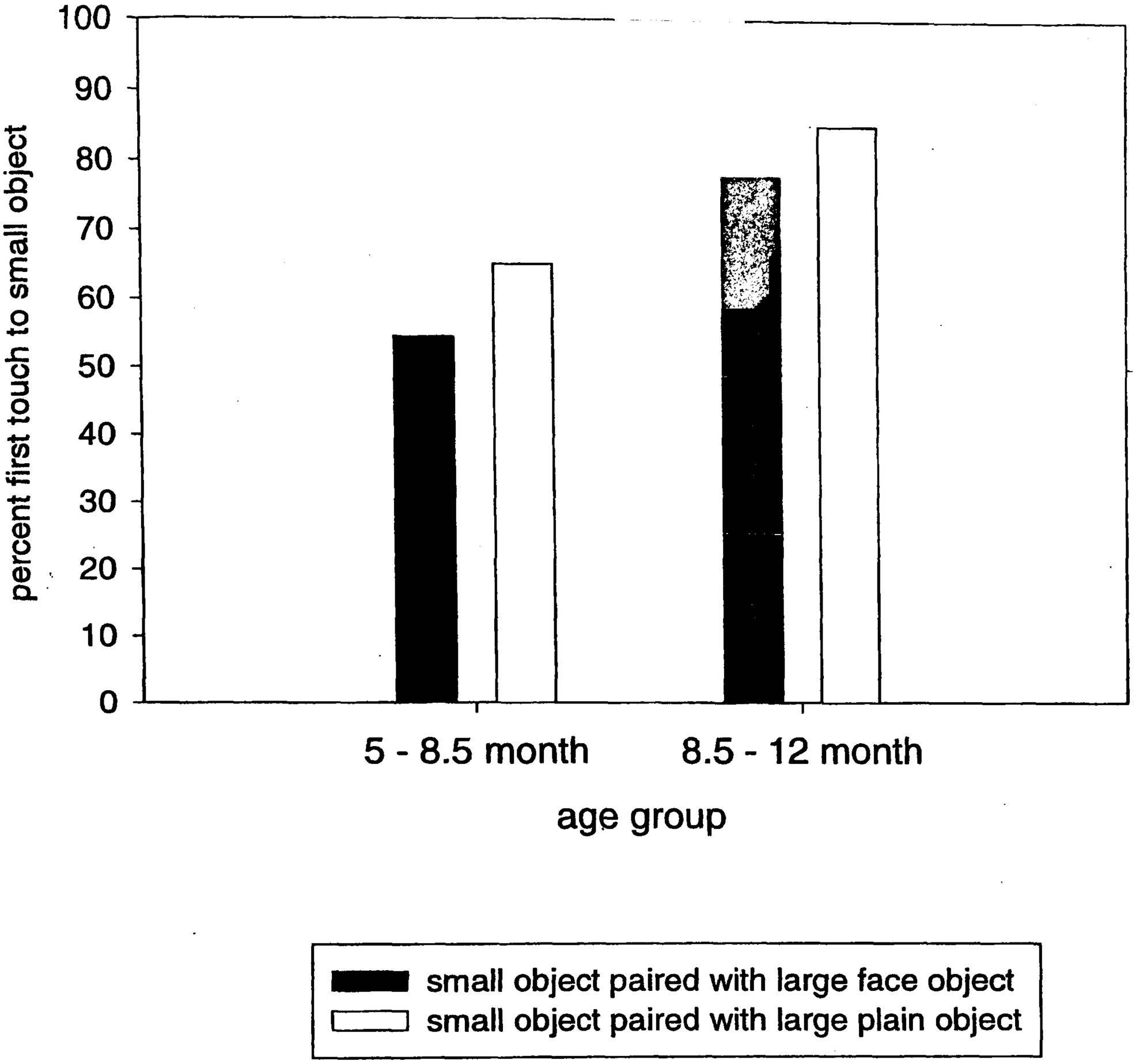


Figure 4.3 Unimanual reaches: Percentage of first touches to the small object when paired with the large face or large plain object

for an age trend in the data was significant, $F(1,23) = 19.7$; $p<0.001$, R-sq = 0.47. The slope of the linear component was positive and significant, $t = 4.4$; $p<0.001$. This regression analysis confirms a developing preference in reaching for the small (graspable) object.

Figure 4.3 shows the proportion of first touches to the small object, broken down by age group. It can be seen that in both age groups the tendency to reach for the small object was reduced when it was paired with the face object. A mixed model ANOVA with age group as the between subjects factor, and object pairing as the within subjects factor was used to test whether the proportion of reaches to the small object was affected by the visual features of the object it was paired with. There was a significant effect of age group $F(1, 22) = 14.1$ $p< 0.001$, confirming that infants in the older age group were more likely to reach for the small object than both the face or plain object. There was also a significant effect of object pairing, $F(1,22) = 5.03$ $p<0.035$. The interaction of object pairing and age group was not significant.

Whilst a significant interaction revealed by the ANOVA analysis can show a difference between age groups in responses to the object pairings, it does not show whether, within a pairing, the level of reaching to one object is greater than chance. One sample t-tests were therefore used to test for preferences within object pairings for each age group. These tests revealed that the level of reaching to the small object was greater than chance level (50%) in both age groups when it was paired with the large plain object, but reaching to the small object was at chance level in the younger age group when it was paired with the large face object.

SL pairing: infants under 8 ½ months, $t(11)= 3.98$; $p<0.003$. Infants over 8 ½ months $t(11)= 9.5$; $p<0.001$.

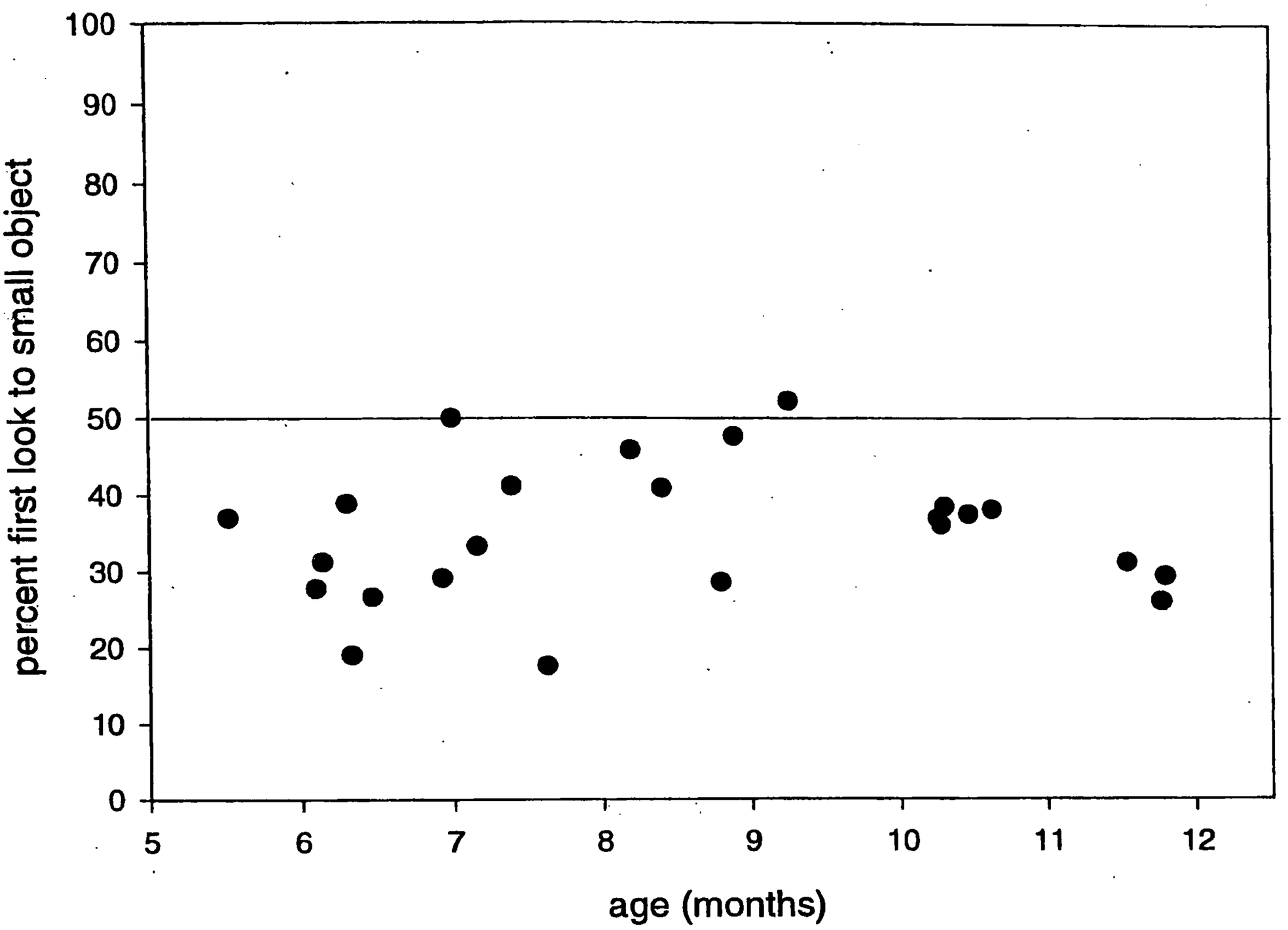


Figure 4.4 Percentage of first looks to small object, by age of subject

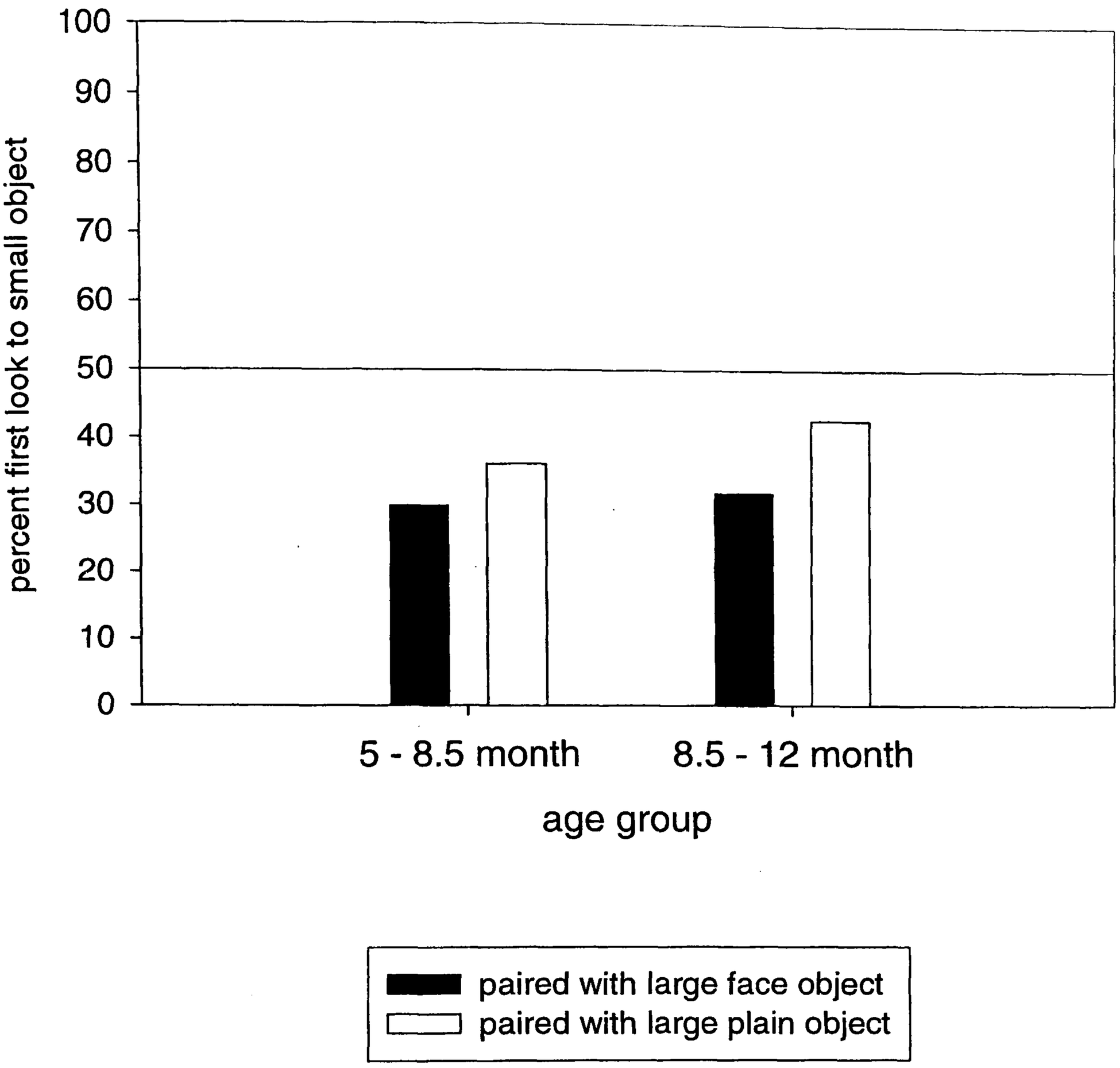


Figure 4.5 Percentage of first looks to the small object
when paired with the large face or large plain object.
Note that figures under 50% indicate a looking preference for larger objects

SF pairing: infants under 8 ½ months, t(11)= 1.1, p<0.3. Infants over 8 ½ months t(11) = -4.3; p<0.001

(one-sample t-tests, test level 50%).

4.3.4. Visual preference (target of first look)

A linear regression was used to model the effect of age on looking behaviour. The predictor variable was age; the dependent variable was the overall proportion for each subject of first looks to the small object. The linear coefficient was positive, indicating that first looks to the small object increased slightly with age, but was not significantly different from zero, $F(1,23) = 0.69$; $p < 0.42$, Figure 4.4 shows the proportion of first looks to the Large object (face or plain), plotted as a function of the age of the subject, and Figure 4.5 shows the same data broken down by age group and object pairing. ANOVA analysis was also used to test the effect of the visual features of the larger object upon looking preferences. There was no significant effect of age group $F(1, 22) = 1.7$, $p < 0.2$, however there was a significant effect of object pairing, $F(1,22) = 4.17$, $p<0.05$. The interaction of object pairing and age group was not significant.

One sample t-tests were again used to test for looking preferences within object pairings. These tests revealed that the level of first looks to the small object was less than chance in both age groups when it was paired with the large face object, but was not significantly less than chance in the older age group when paired with the large plain object.

SL pairing: infants under 8 ½ months, t(11)=3.17; p<0.009. Infants over 8 ½ months t(11)= 1.93; p<0.08

SF pairing: : infants under 8 ½ months, t(11)=4.35, p<0.001. Infants over 8 ½ months t(11) = 4.94; p<0.001.

Thus looking preferences to the LS pairing show a similar pattern to that observed in previous experiments, with a significant preference for the large object being seen only in infants under 8 ½ months. The addition of a face to the large object however, increases the likelihood of a first look in both age groups.

4.3.5. Relationship between looking and reaching

In order to test whether the difference in the proportion of reaches to the face object was driven by looking preference, the proportion of trials in which the object first fixated was the same as the object finally touched was calculated for each object. The results are presented in Table 4.1 A repeated measures ANOVA comparing the proportion of reaches to each object which were look-touch congruent in each age group showed that there was a significant effect of object ($F(2,46) = 7.9$, $p<0.001$), but no significant interaction between age group and object. Thus infants are most likely to reach for the object they first looked at when that object is visually salient.

Table 4.1 Percentage of reaches to each object which were *look-touch congruent*.

Age group	Small	Large Face	Large Plain
5-8.5	49	82	70
8.5-12	50	74	53

From observation of the infants it was apparent that in some trials (n = 53), the infant started the reach looking at one object, but finally touched a different object. The target of these (*reach incongruent*) trials was in the great majority of cases the small object (see table 4.2). Thus infants were much more likely to initiate a reach towards a large object, then switch to the small object , than vice versa.

Table 4.2 Proportion of *reach incongruent* trials in which the target of the reach was the small object.

Age group	SF Pairing	SL Pairing
5-8.5 months	10/12	6/9
8.5-12 months	12/12	18/20

4.3.6. Two-handed reaches

Of 54 bimanual reaches overall, 31 were made by infants under 8 ½ months, 23 by infants over 8½ months. Thus 86.4% of reaches in infants under 8 ½ months were one-handed, and 90.7% in infants over 8 ½ months). The target of two-handed reaches is presented in Table 4.3

Table 4.3 Proportion of bimanual reaches to the small object in each pairing

Age group	SF pairing	SL Pairing	total
5 - 8.5 months	7/16 (44%)	8/15 (53%)	15/31 (48%)
8.5 - 12 months	8/15 (53%)	6/8 (75%)	14/23 (61%)

From this table is apparent that bimanual reaches were equally likely to be made to the small or large object in the youngest age group, whereas in infants over 8 ½ months majority of bimanual reaches were towards the small object. This preference was only expressed, however, when the small object was paired with the face object, and then only in a few trials.

4.3.7. Kinematic analysis

Data is presented from 184 one-handed reaches. Means and standard deviations of kinematic variables are presented in tables 4.4 - 4.7. Each dependent variable was entered into a 3x2 factorial ANOVA, with age group, object and as independent

variables. There were no significant differences between reaches made to the three objects, or between infants of different ages. However, from the tables below it can be seen that results were at least numerically in line with those of experiment 1. Infants in the youngest age group reached more slowly and spent longer in deceleration than the older infants.

Differences between ipsilateral and contralateral reaches were analysed using paired t-tests. Maximum hand speed was again higher when reaching contralaterally than ipsilaterally ($t(13) = 2.3$, $p<0.037$. None of the other measures showed significant differences between ipsilateral and contralateral reaches.

It was also found that reaches in which the target of the reach was the same as the initial visual preference (look-congruent reaches) had a higher peak hand speed than reaches in which the target of the reach was different from the initial visual preference:- $t(13) = 2.16$, $p<0.05$. (see table 4.7).

Table 4.4. Means and standard deviations of kinematic variables, by *age group*

	5 - 8.5 months			8.5 - 12 months		
Dependent variable	Mean	sd	n	Mean	sd	n
duration (msec)	**1209.53**	569.88	128	**1328.93**	589.19	56
peak hand speed (mm/s)	**410.57**	196.06	128	**348.38**	143.14	56
no. of peaks	**2.29**	1.32	128	**2.23**	1.13	56
deceleration time (msec)	**765.00**	457.79	128	**908.21**	614.55	56
straightness index	**1.72**	0.95	128	**1.48**	0.77	56
maximum deviation (mm)	**34.07**	23.10	128	**28.90**	18.01	56

Table 4.5. Means and standard deviations of kinematic variables, by *object touched*

	object touched								
	small			large face			large plain		
Dependent variable	Mean	sd	n	Mean	sd	n	Mean	sd	n
duration (msec)	**1312.64**	581.62	125	**1065.88**	523.96	34	**1156.80**	578.44	25
peak hand speed (mm/s)	**380.87**	176.44	125	**425.46**	219.68	34	**399.55**	164.82	25
no. of peaks	**2.48**	1.34	125	**1.71**	0.94	34	**2.00**	0.96	25
Deceleration time (msec)	**847.36**	530.58	125	**739.41**	416.61	34	**708.80**	538.18	25
straightness index	**1.72**	1.03	125	**1.44**	0.47	34	**1.56**	0.62	25
Maximum deviation (mm)	**34.00**	23.12	125	**26.85**	18.26	34	**32.65**	18.26	25

Table 4.6. Means and standard deviations of kinematic variables, by *side of reach*

	side of reach					
	ipsilateral			contralateral		
Dependent variable	Mean	sd	n	Mean	sd	n
duration (msec)	**1234.21**	552.91	145	**1289.23**	664.50	39
peak hand speed (mm/s)	**367.98**	161.38	145	**479.62**	230.93	39
no. of peaks	**2.27**	1.27	145	**2.28**	1.23	39
deceleration time (msec)	**808.28**	509.73	145	**809.74**	532.42	39
straightness index	**1.65**	0.93	145	**1.63**	0.81	39
maximum deviation (mm)	**30.69**	21.35	145	**39.23**	22.21	39

Table 4.7. Means and standard deviations of kinematic variables, by *look-touch congruence*

	congruent			non-congruent		
Dependent variable	Mean	sd	n	Mean	sd	n
duration (msec)	**1155.00**	620.62	100	**1354.05**	502.44	84
peak hand speed (mm/s)	**410.68**	196.13	100	**368.99**	165.44	84
no. of peaks	**2.07**	1.29	100	**2.51**	1.19	84
deceleration time (msec)	**736.20**	509.01	100	**894.48**	507.76	84
straightness index	**1.61**	0.86	100	**1.70**	0.95	84
maximum deviation (mm)	**32.71**	22.10	100	**32.24**	21.48	84

4.4 LONGITUDINAL STUDY

4.4.1. Details of visits

4 infants took part in the study. Jarod made 11 visits at two-weekly intervals between the ages of 5 ½ months and 12 months. Luke attended 8 times between the age of 5 ½ and 11 months with data being collected on 7 of these occasions. Emily attended 6 times between the ages of 4½ and 9 months, but on 2 occasions became fussy and did not do the experiment (including the first visit). Thomas attended 17 times, between the ages of 4.8 months and 12 months, data is presented from 12 of these sessions.

4.4.2. Results

The proportion of looks and reaches to the face and large plain objects is presented in figures 4.6 to 4.13, broken down by object pairing. The first point that is apparent from these graphs is that all infants show a decrease with age in the proportion of reaches to the larger objects except for Emily, who showed a preference for the small object right from the start, at 5½ months. Thomas showed a decrease in reaches to the

larger objects until 7 ½ months at which point he became able to pick up the larger objects. After this age the frequency of reaches to larger objects increased again.

Figure 4.14 compares the proportion of reaches to the small object with the proportion of 'successful' grasps of the larger object. (A successful grasp was defined as one in which the object was grasped and raised from the table with one hand). It should be noted that none of the other three infants successfully picked up the large objects with one hand in any of the sessions. On one of Jarod's visits (at 9.2 months) he switched to exclusively bimanual reaching and reached for the face object on the majority of trials in which it was presented.

Three of the four infants showed an overall preference for looking first at the larger object of the pair. However, there is no clear difference in the number of first looks to the face or large plain object except for the fact that all the infants looked most at the Face object on their first visit.

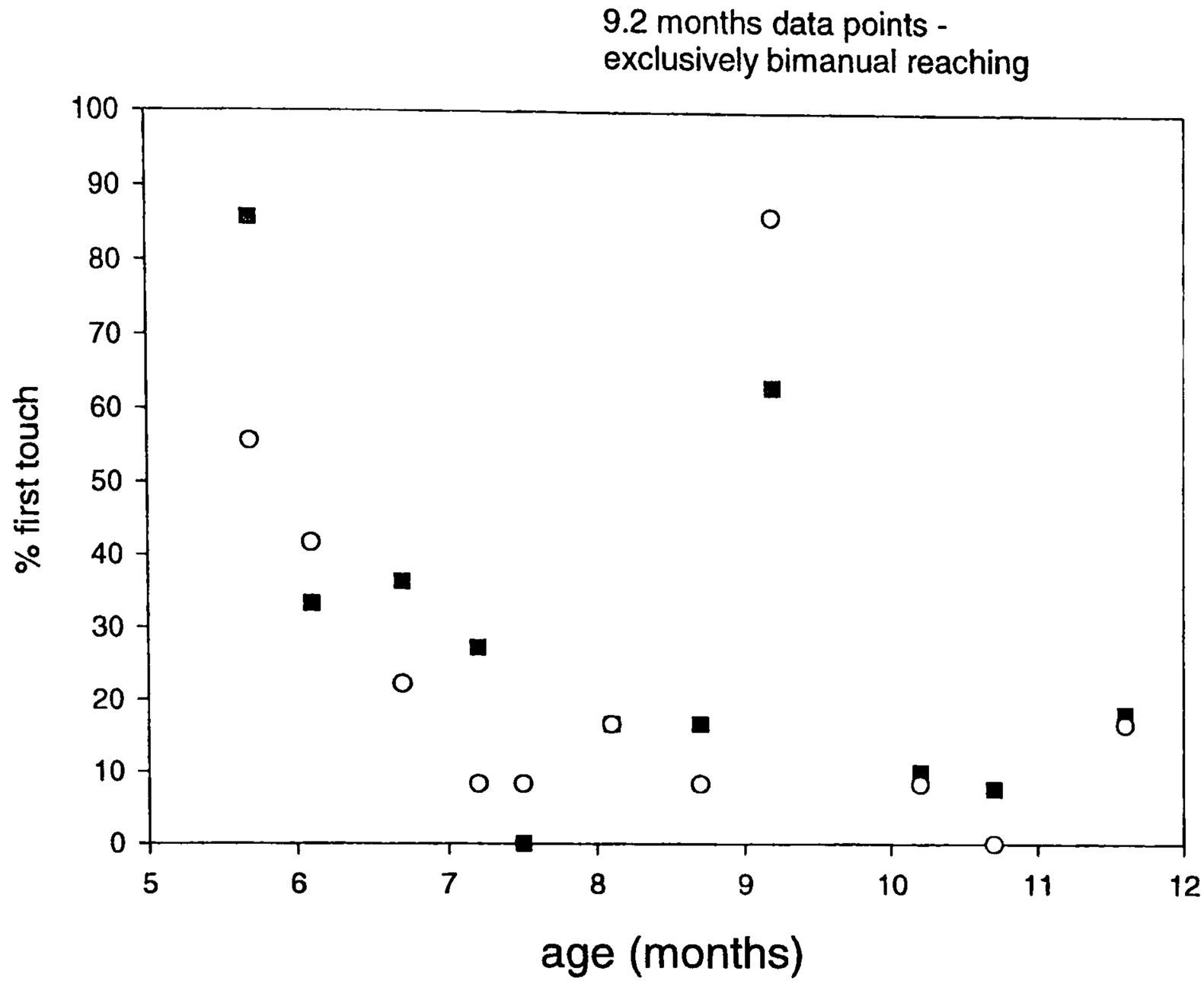


Figure 4.6 Jarod: Proportion of first touches to the large face and large plain objects

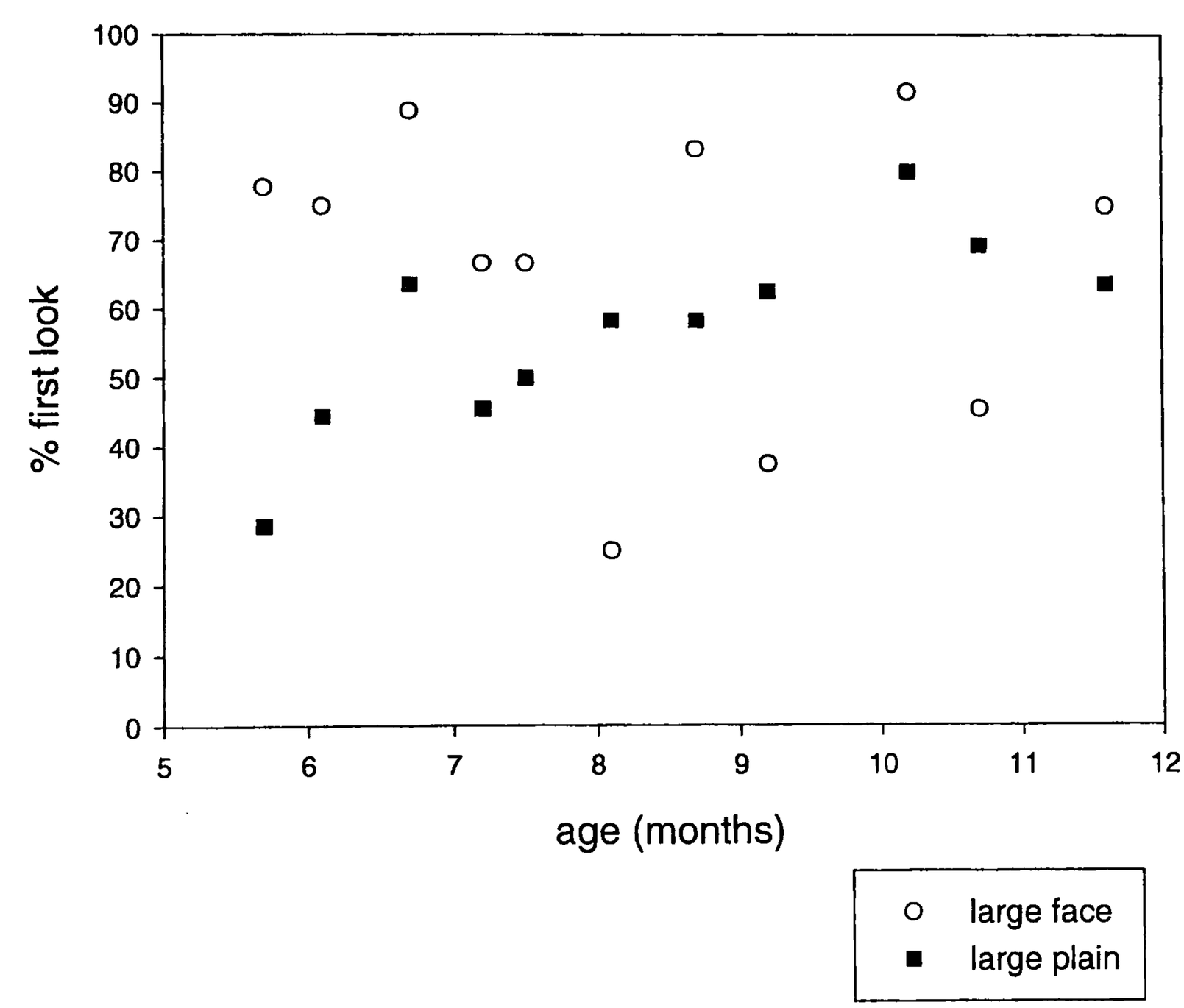


Figure 4.7 Jarod: Proportion of first looks to the large face or large plain object.

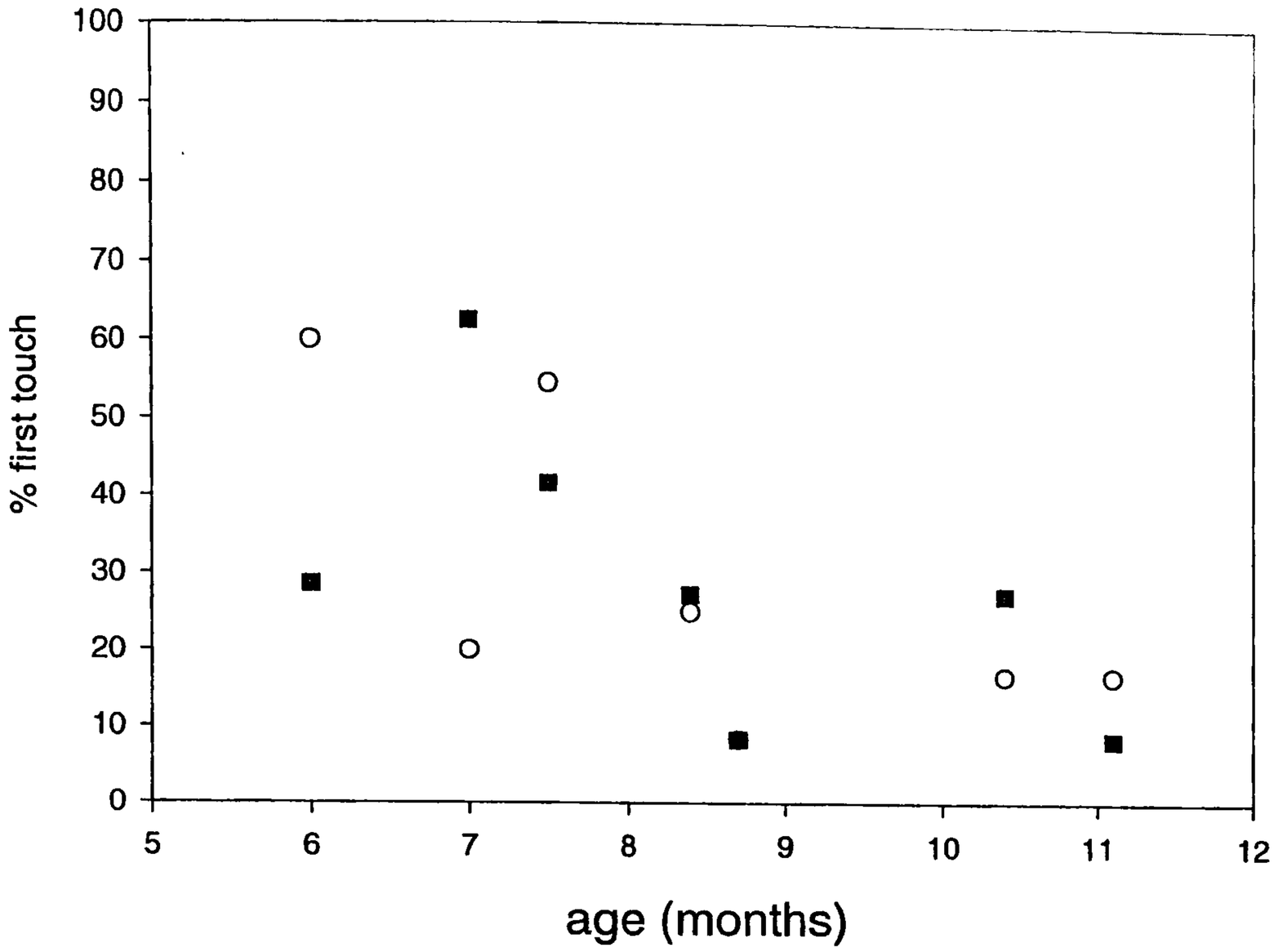


Figure 4.8 Luke: Proportion of first touches to the large face and large plain objects

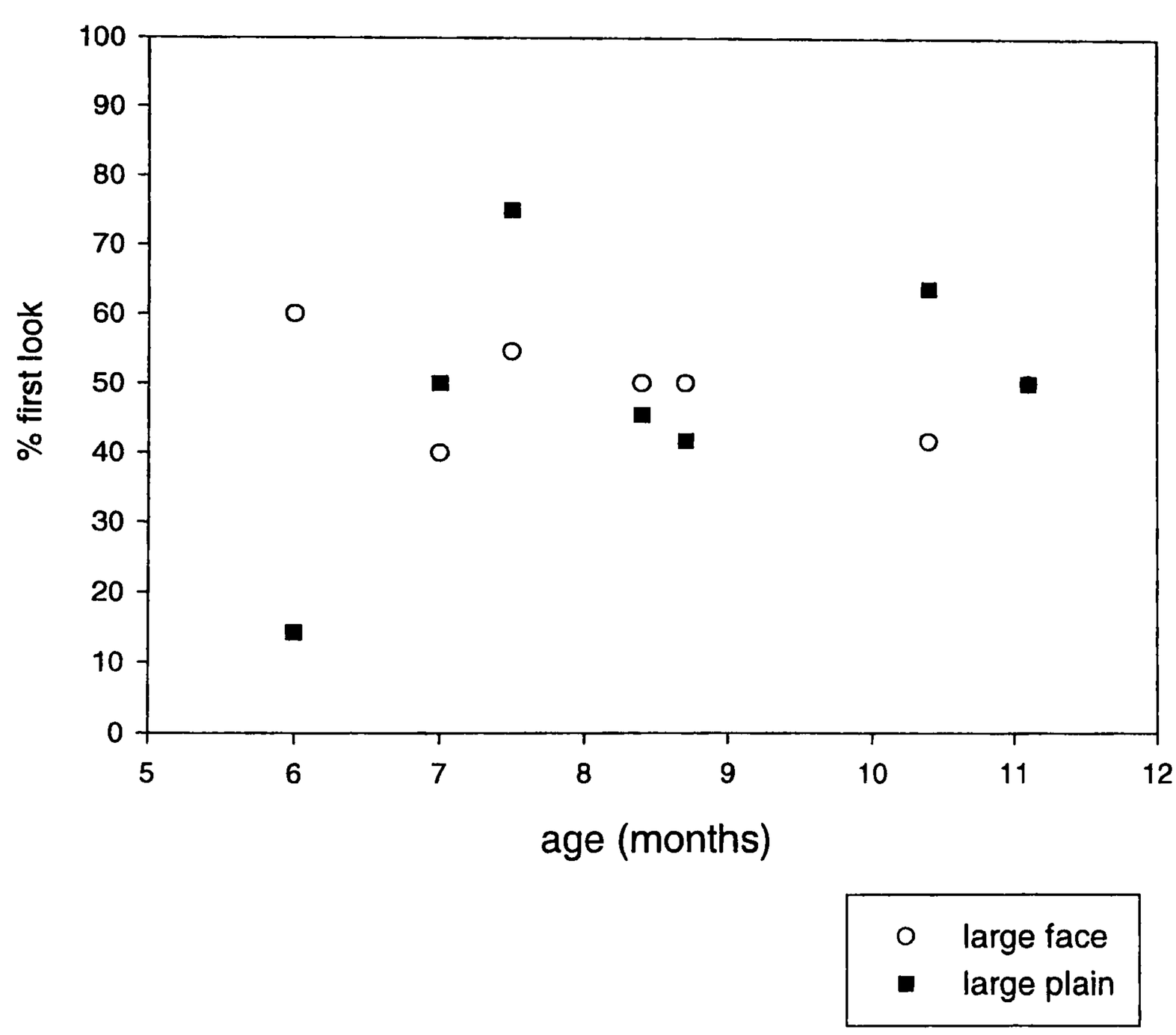


Figure 4.9 Luke: Proportion of first looks to the large face or large plain object.

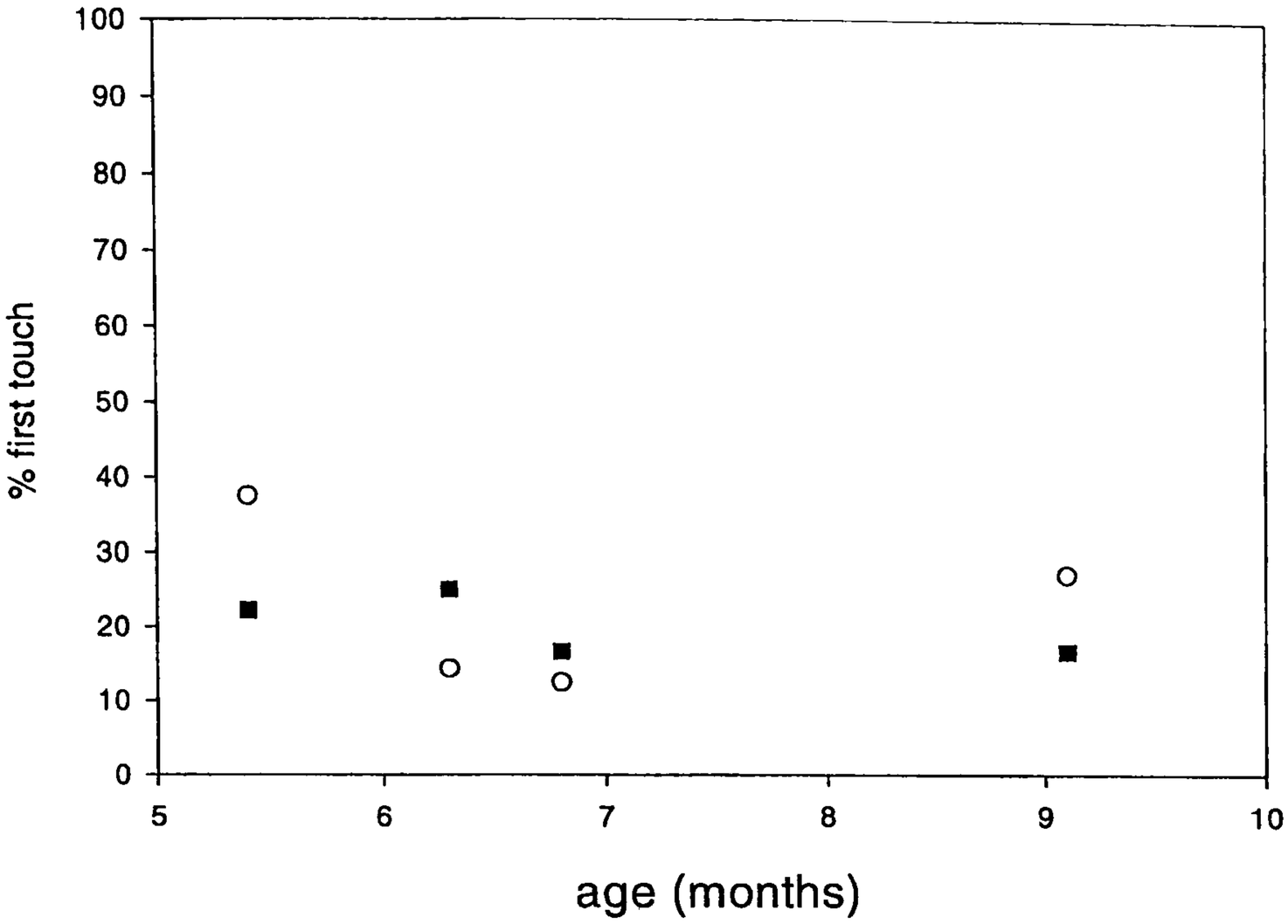


Figure 4.10 Emily: Proportion of first touches to the large face and large plain objects

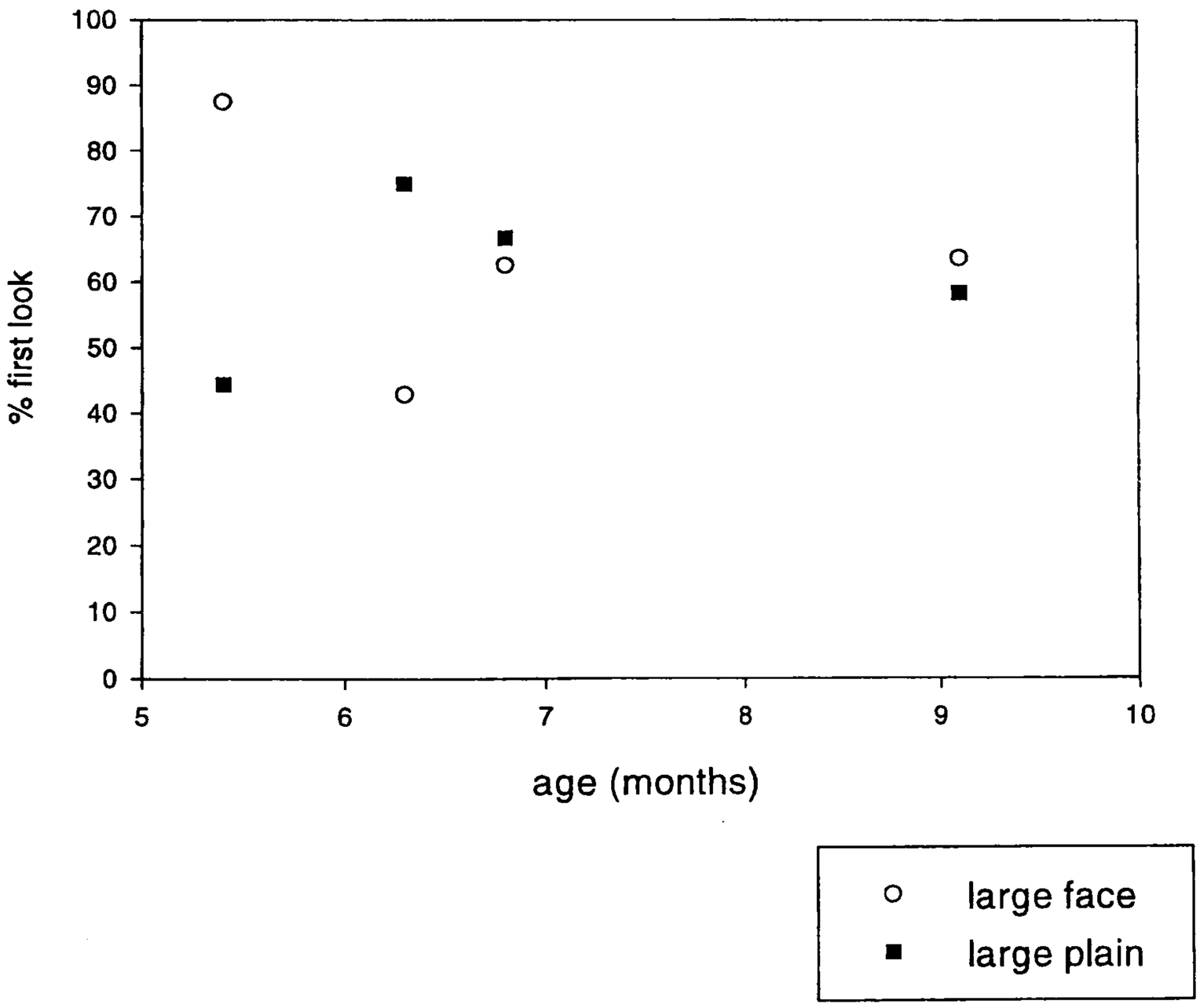


Figure 4.11 Emily: Proportion of first looks to the large face or large plain object.

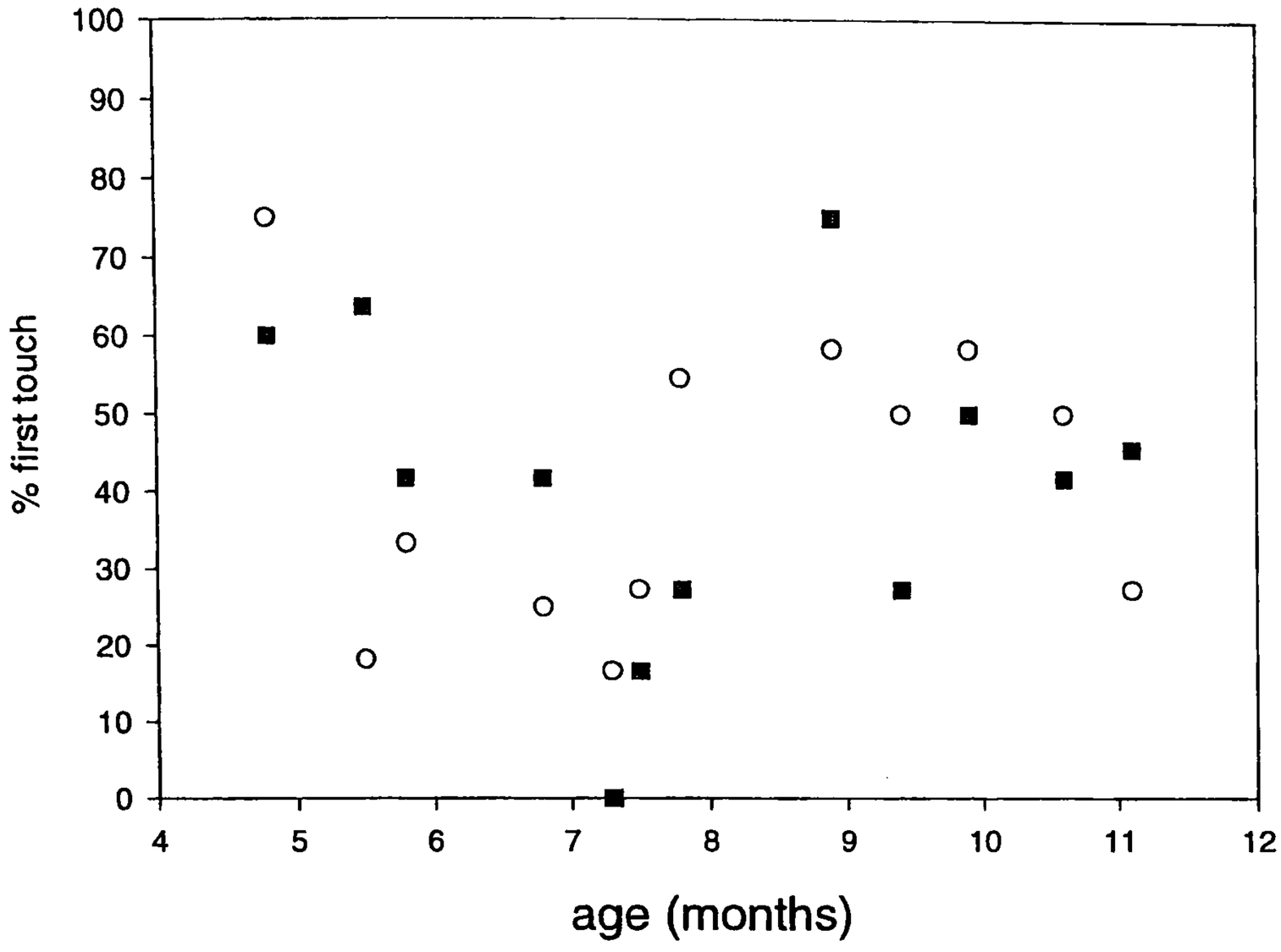


Figure 4.12 Thomas: Proportion of first touches to the large face and large plain objects

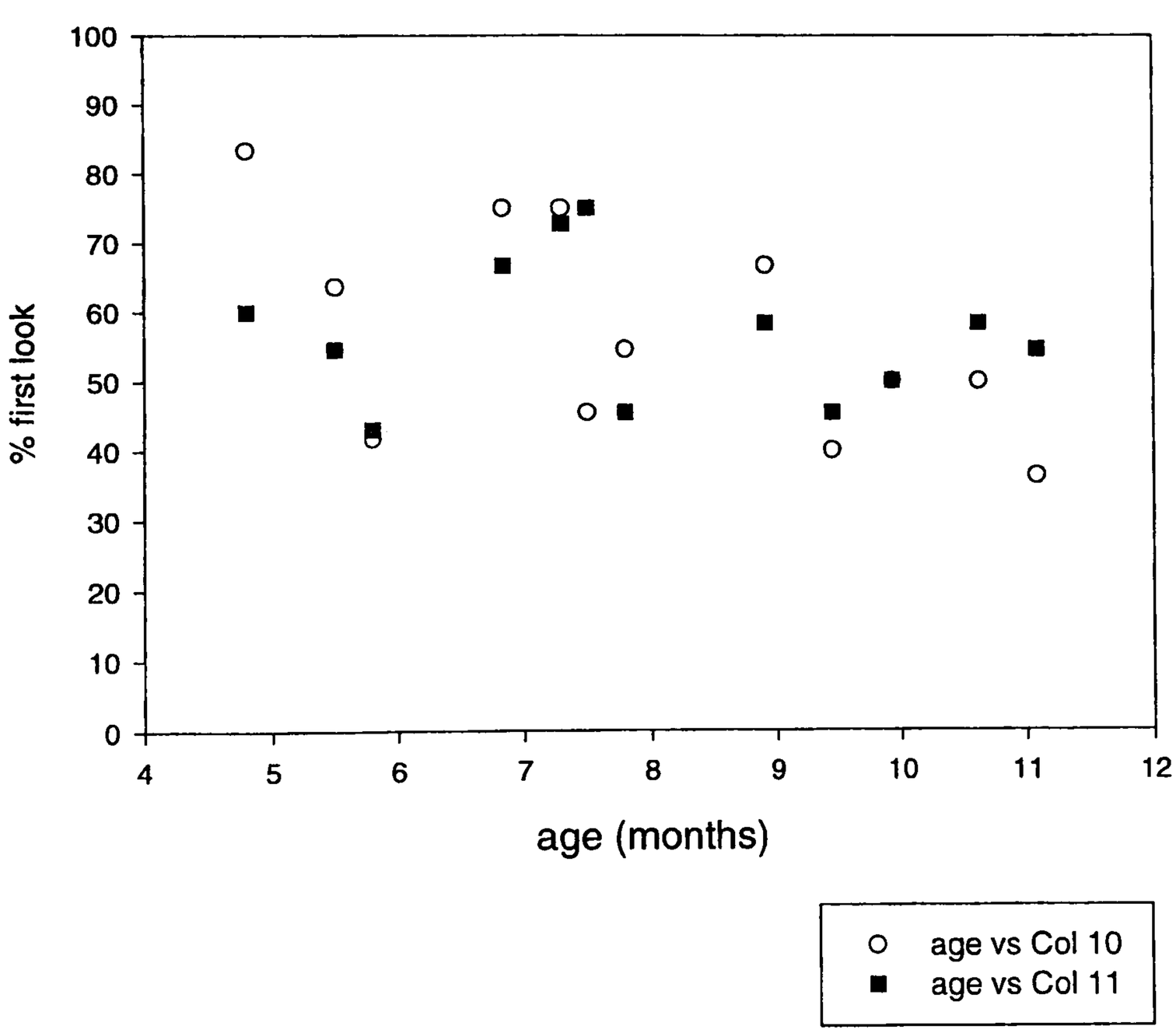


Figure 4.13 Thomas: Proportion of first looks to the large face or large plain object.

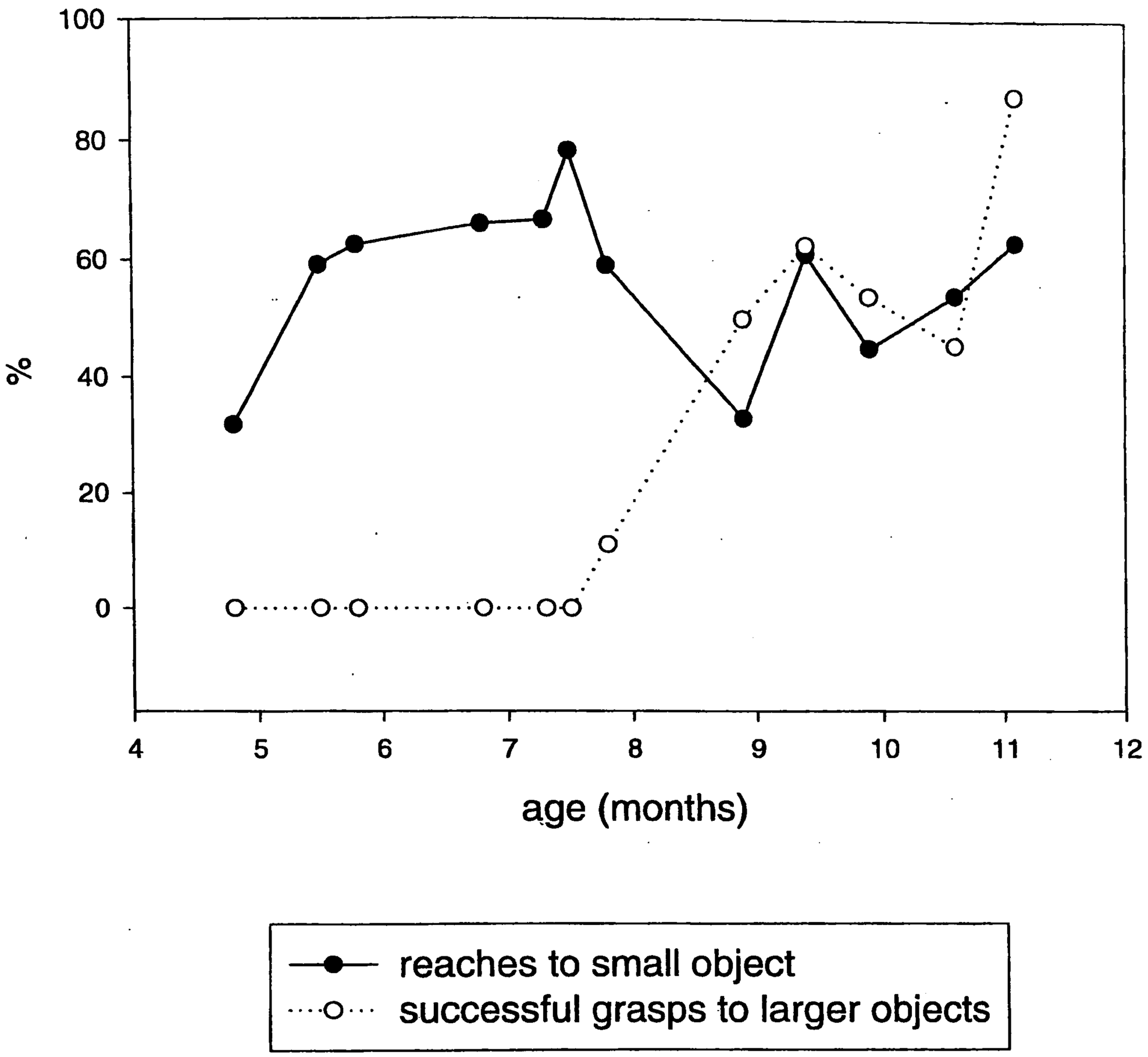


Figure 4.14 Thomas: Percentage of first touches to small object compared with successful grasps to the larger objects.

The results of this study show that individual infants follow the developmental trend found in the cross-sectional data - the preference for reaching to smaller objects increased soon after the onset of goal-directed reaching, but declined once the infant was able to pick up the larger objects. However, this study also highlights the individual differences that underlie the grouped data presented in the other experiments in this thesis. Infants do not develop the preference for graspable objects (or lose it) at the same age. Emily showed the preference very early (5½ months) and Thomas was able to grasp the large objects at 9 months.

The effect of varying the visual features of the larger object was less clear. Whilst there seemed to be an overall preference for looking at the larger object of the pair, and reaching to the smaller object, there was no consistent difference between the frequency of first looks or reaches to the face or large plain objects. It is perhaps indicative that all the infants in this study looked at the face object most often on their first visit. The extra attractiveness of the face object in comparison with the large plain object may depend upon a response to novelty, which declines with repeated experience of the objects. This highlights the general methodological point that it is difficult to use longitudinal studies to study any effect that depends upon a response to novelty.

4.6 DISCUSSION - CROSS-SECTIONAL STUDY

4.6.1. Visual preference

When the small object is paired with a large plain object, looking preferences show a similar pattern to that observed in previous experiments, with a significant preference for the large object being seen only in infants under 8 ½ months. However, when a schematic face is added to the large object, the likelihood of a first look is significantly above chance level in both age groups. This result is not surprising, given

that even newborns have been shown to prefer to look at patterned and face-like stimuli (Fantz, 1961). However, once infants are reliably able to identify objects which are easy to manipulate, increasing the visual salience of an object which is too large to grasp ought to be irrelevant to reaching behaviour. Is the looking and reaching behaviour in fact uncoupled in this way?

4.6.2 Reaching preference (bimanual reaches)

In bimanual reaches, there was again no consistent tendency to use two hands to reach for larger objects. In fact, the majority of bimanual reaches were to the small object in the older age group. The pattern of reaching was similar to that observed in one-handed reaches, with less reaches to the small object being made when it was paired with the face object. This might indicate that in a few trials, the extra visual salience of the face object induced some infants to switch to a two-handed reach in order to grasp it. However, the low frequency of bimanual reaches indicates that this was not a common occurrence.

4.6.3. Reaching preference (one-handed reaches)

Infants again preferred to reach with one hand, and the frequency of one-handed reaches for the small object increased with age, as in Experiment 1. When presented with two objects that differed only in size, infants in both age groups preferred to reach for the graspable object. This demonstrates that these infants were able to make a choice of object based upon its potential for manipulation. However, when the larger object had a face printed on it, the proportion of reaches to the small object was reduced (indeed, in infants under 8 ½ months the face and the small objects were equally likely to elicit a reach, because the preference for reaching to smaller objects was not as strong.). This is consistent with the hypothesis proposed in the last chapter,

that maturation of the ability to select and reach for an object may depend upon a dissociation during development of visual processing streams subserving object-related action from those related to visual orienting. Part of an infant's development in exploring the world around him or her is learning to assign appropriate actions to objects - looks to distant or unwieldy objects and manual exploration of smaller, closer objects. Whilst looking and reaching systems seem to be able to operate quite independently when infants over 8 ½ months are presented with objects which differ only in size, in this experiment, we have increased the likelihood of a reach to a difficult-to-manipulate object by increasing its visual attractiveness.

Can we speculate about which neurodevelopmental processes underlie this behaviour? Firstly, it is necessary to consider what processes are involved in selection for action in infants. The proposal made in the previous chapter was that the ability to visually scan a scene and select a suitable target for action depends not only upon *target selection* processes (the inhibition of all but one of the potential actions elicited by a visual scene), but also on *inhibition between action systems*.

(a) Target selection processes

The target selection process might be done in two (not necessarily mutually exclusive) ways. Firstly, the object which is the current focus of visual attention might be compared with representations derived from prior experience. A second possibility is that when visual attention is paid to an object, an implicit grasping action is also prepared, but not necessarily executed. Feedback from this implicit action preparation could provide information about an object's potential for manipulation without the need to access stored representations. (see section 1.5).

(b) Inhibition between action systems. As reviewed in section 1.8.2, there is evidence from adult behavioural studies, neurophysiological studies and also from a

neuropsychological patient (see Carey *et al.* 1997), that whenever the target of fixation changes, a reach is prepared that would carry the hand to the same target (Snyder *et al.* 2000). In this account, independent activation of reaching and looking, i.e. the ability to look to one place but to reach to another, therefore depends upon inhibition between looking and reaching systems.

There are therefore a number of possible explanations for infants' behaviour in this experiment.

Infants might have immature representations of object attributes. Infants might reach to the face object rather than the small object because they have weak or unstable representations of what is a 'graspable' object. In this case, inhibition signals based on these representations may be too weak or erratic to reliably inhibit reaches to the most visually salient object.

Infants might have an immature or undifferentiated visual processing streams specialised for action. Infants might find a reach to the face object more difficult to inhibit because action control circuits are not yet fully specialised for the processing of reach-related attributes. In this account, feedback from implicit action processing in the action stream would be a poor indicator of graspability.

Look and reach systems in infants may not be fully uncoupled. Infants might reach to the face object is more often than the large object because they tend to look where they reach, and this tendency is exaggerated when the visual salience is increased.

Can one decide between these accounts on the basis of the current evidence? The present data most strongly suggest that visual orientation and reaching are yoked in infancy. There is evidence from this study that the direction of the reach may be influenced by where the infant looks first in each trial. Reaches in which the target of

the first look and the target of the reach were the same (look-touch congruent reaches) were more likely to be made to the Face object. In addition, kinematic evidence shows that look-touch congruent reaches reached a higher peak hand speed than reaches where the target of first look and reach target were not the same. Thus it seems that reaches to the most visually salient object are sometimes driven by a 'look/reach' mechanism, involving both eye and arm movements which may, as suggested in the last chapter, be a general orienting response which is adaptive for the infant's initial exploration of the world. The current data certainly implies that reach mechanisms in the infant can be activated by two sources, one which 'knows' about grasp affordances and one which does not. . However, true flexibility in the choice of object to reach for would require the ability to inhibit such a response. Direct evidence for inhibition of reaches to the larger objects is provided by those trials where the infant switched the target of the reach after reach onset. The direction of this mid-reach switch was almost exclusively from large to small, as if the infant had started to reach impulsively to the most visually salient object, but the inhibition signal from circuits computing graspability did not take effect until after the start of the reach. This implies that information about an object's potential for manipulation feeds into a slower target selection process operating in parallel with, and occasionally in conflict with, a less specifically tuned orienting system.

This data is in accordance with that of Smith *et al.* (1999), who have shown that target selection during an A-not-B task can be influenced by drawing an infant's visual attention to one side or another just before the reach starts. There are some parallels between the results of the current experiment and those from the A-not-B task, in that in the reaching version of the A-not-B task infants fail to use knowledge about objects that they can display in other situations, such as a violation-of-expectation test of object

permanence (e.g Bailleargeon and Graber (1988)). In the current experiment, infants seem use their 'knowledge' about objects less reliably in trials where the competing object is more visually attractive. Rather than looking for explanations of such effects in the status of object representations, Smith at al., (1999) propose that infants fail to reach for the correct location because of a combination of factors which interact during a reaching task, such as the tendency to perseverate, and the tendency for reaches to follow the direction of gaze. As Smith *et al.* point out, the processes of scanning the visual scene, selecting a target, preparing and enacting a reach are not necessarily sequential, discrete steps, but overlap in time. In the developing brain, which may still be in the process of functional differentiation, the parallel nature of visuomotor processing may lead to unpredictable interactions between the different systems that determine motor output.

5 Planning and control of movement in children with Williams' syndrome

5.1 INTRODUCTION

Williams syndrome (WS) is a genetic disorder with incidence in the population of around 1:20,000 births. Transmission is autosomal dominant but most cases arise spontaneously. The medical signs associated with WS are hypercalcaemia in infanthood (greater than normal levels of calcium in the blood, which results in abdominal pain, muscle pain and anorexia), supervalvular aortic stenosis (SVAS, a narrowing of the arteries in the aorta), characteristic 'Elfin' facial features, and mental retardation along with a distinctive cognitive profile. Morris (1999) describes the WS cognitive profile (WSCP) as follows:

The cognitive profile is distinctive, consisting of strengths in auditory rote memory and language, but extreme weakness in visuospatial constructive cognition. As a result, children with WS usually score higher on verbal subtests than on tests measuring visuospatial construction. Academically, individuals with WS perform relatively well in reading, and adults may read at the high school level, though the range of achievement is wide. There is significant difficulty with writing, drawing, and mathematics; however, many adults with WS are able to perform simple addition.

Until 1993, diagnosis of WS was based upon based on the presence of these behavioural and physical characteristics, however it is now known that in 99% of patients with classic signs of WS there is a microdeletion of the WS critical region of chromosome 7 (chromosome band 7q11.23) which includes the elastin gene (ELN) (Ewart, Morris, and Atkinson,. 1993). Altogether 18 genes have been identified in the deletion region on chromosome 7 (Korenberg *et al.* 2000). Figure 5.1 shows these genes, as mapped by Korenberg *et al.* along with the extent of the typical deletion in WS.

A number of these genes are expressed in the brain. Galaburda *et al.* (1996) report that Purkinje cells in the cerebellum of normal human brains was stained by an antibody to elastin, whereas this was not the case in two Williams syndrome brains. The STX1A gene codes for part of the synaptic mechanism in the brain (Tassabehji *et al.* 1999), and LIM kinase1 is expressed in the cerebral cortex (Mervis *et al.* 1999). Gene specific effects have been clearly identified for the elastin gene, which is associated with the arterial disorders and connective tissue disorders in WS. Individuals with only the elastin gene deleted suffer from these disorders but have none of the other characteristics of WS (Li *et al.* 1997; Tassabehji *et al.* 1999). However, the evidence from studies which have attempted to determine the extent of the deletion necessary to cause the full WS profile is somewhat contradictory. Korenberg *et al.* contend that the deletion of a small set of genes at the end of chromosome 17 seems to be sufficient to cause the typical cognitive and facial features of WS. Thus, Tassabehji *et al.* (1999) report on a case CS, who has heart disease but no cognitive or facial features of WS, who has a deletion of FZD9 to RFC2 inclusive (see Fig. 5.1). Two other patients had smaller deletions which included LIM kinase1 and elastin who did not display any

relative deficit on spatial construction tests, had normal IQ and did not display the characteristic facial features of WS.

Korenberg *et al.* also report on a case who has a deletion of the region including FZD9 to RFC2 inclusive, who showed mild cognitive impairment, but not the WSCP. Further evidence that it is the genes towards the end of the deleted region which are critical to at least the facial features of WS is provided by Botta *et al.* (2000) who have identified two children who have the genes after but not including STX1a deleted. Both of these children have the heart problems and facial features characteristic of WS. One child was only 2 years old, so the cognitive profile could not be ascertained. The other 6 year old child was reported to have the personality characteristics of WS along with 'visuoperceptual and visuomotor difficulties', although details of testing were not provided in the paper.

However, Frangiskakis *et al.* (1996) have claimed that the deletion of just elastin and LIM kinase1 is associated with visuospatial impairment in WS. These researchers studied 13 individuals who had small deletions in the WS critical region. These individuals were drawn from two sets of related individuals, one set with a larger deletion than the other. The group with the smaller deletion had only elastin and LIM kinase1 deleted. These individuals nevertheless displayed the WS cognitive profile (WSCP), which was defined by these researchers as a relative impairment on spatial construction tests when compared with other sub-tests of the Differential Ability Scales or British Ability Scale (Elliot, 1990, 1997). Mervis *et al.* (1999) (from the same group as Frangiskakis) argue that the individuals taking part in the Tassabehji study were of greater average verbal intelligence than those in the Frangiskakis study. Their contention is that these individuals may have had visuospatial problems, but may have been making greater use of verbal strategies to mediate their performance on the pattern

construction tasks. Korenberg *et al.* on the other hand, point out that one of the individuals studied by Tassabehji *et al.* was an engineering student, and therefore unlikely to be a typical WS case. They believe that whilst deletion of LIM kinase1 may be associated with subtle visuospatial problems, it is not sufficient to cause the full WSCP.

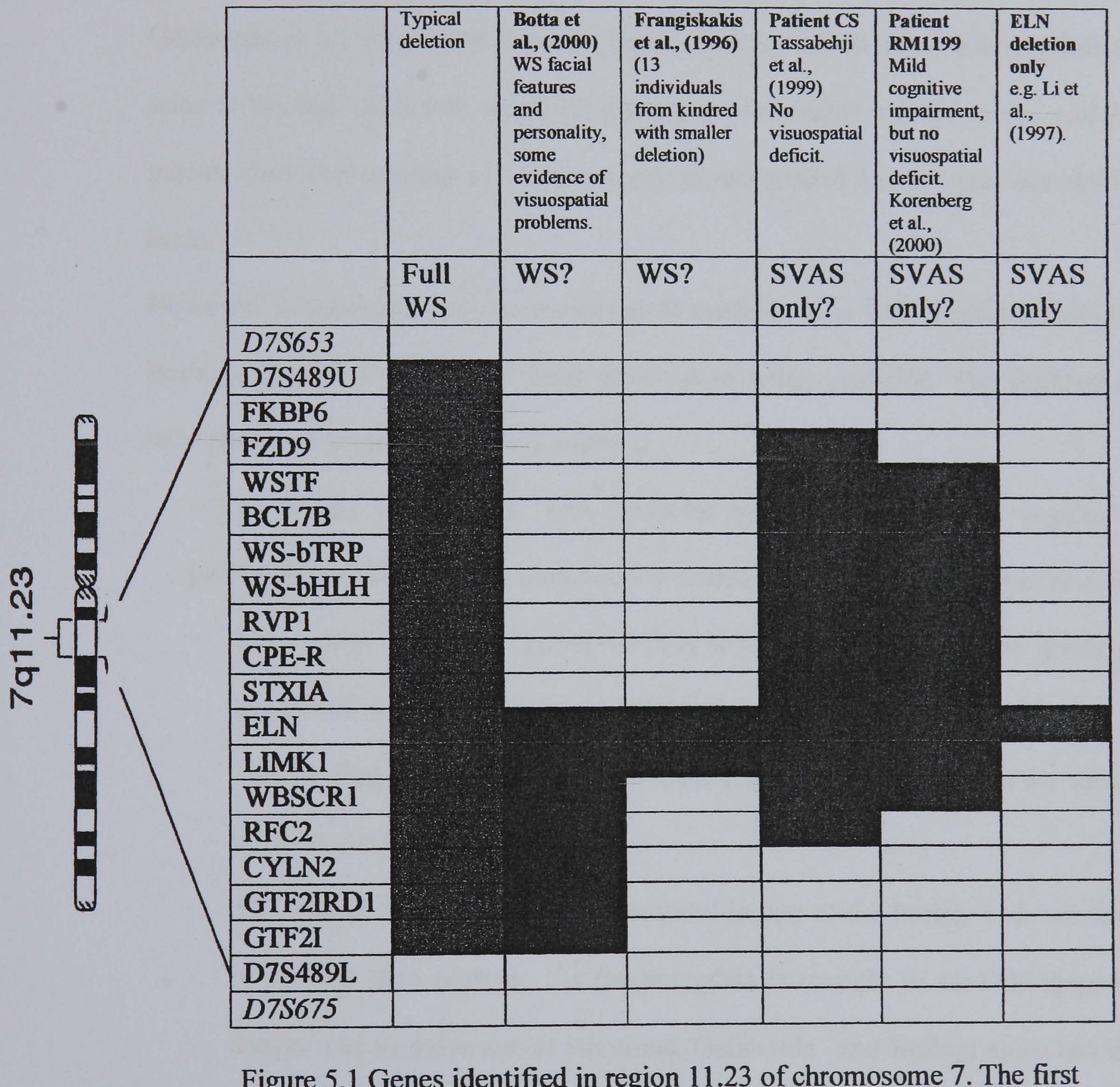


Figure 5.1 Genes identified in region 11.23 of chromosome 7. The first column shows the area typically deleted in WS. Other columns show smaller deletions which in some cases give rise to the full WS syndrome and in other cases to SVAS only.

5.1.1. Brain morphology in WS.

Galaburda *et al.* (1994) reported abnormal clustering and orientation of neurons and decreased myelination in the WS brain along with an increase in cell packing density. Galaburda *et al.* suggested that the increased cell density and incomplete myelination in the WS brain was evidence for neurodevelopmental immaturity. However there was also evidence of abnormal connectivity and layering of the cortex. Galaburda *et al.* speculated that one mechanism by which these abnormalities might arise is through abnormal levels of calcium in the blood inhibiting the cell-pruning mechanisms that operate as connectivity is established in the typically developing brain.

However, a more detailed neuroanatomical analysis of 4 WS brains (Galaburda and Bellugi, 2000) led to some of these conclusions being qualified. The findings of this later study can be summarized as follows:

- The brains were small, with posterior parietal and occipital regions being particularly reduced in size compared to normal brain (see also Reiss *et al.* (2000)).
- The central sulcus did not extend fully to the hemispheric fissure, giving rise to an unusual formation of the superior-parietal lobule and the dorsal frontal gyrus. This finding is interesting, as it is these regions of the brain that are thought to mediate visuo-spatial abilities.
- The size of the amygdala was measured in one of the brains, and was found to be smaller than normal. As the amygdala is thought to mediate responses to danger and aversive social emotions, Galaburda and Bellugi speculate that its reduced size may be related to the unusual lack of shyness seen in many children with WS.

- In addition, a more detailed analysis was carried out of the density and distribution of cells in the various cortical layers. Whilst in Galaburda's previous study the impression was of increased neuronal density, on inspection at a greater level of magnification it was apparent that this impression was caused by an increase in glial cells, which could not be distinguished from small granular neurons at low powers of magnification. In fact, there was, if anything, a decreased cell packing density in the samples studied under high-power magnification.
- The brains studied did not show the asymmetry that is normally present in the planum temporale (a region on the upper surface of the temporal lobe that includes the classical speech area of Wernicke. It is larger on the left side than the right in the majority of humans).
- One of the brains was examined in serial sections. This analysis revealed many small infarcts, too small to be picked up by MRI, particularly in the dorsal parts of the parietal lobe. This finding raises the interesting possibility that the vascular problems that people with WS are prone to, coupled with a greater vulnerability to damage in the dorsal-parietal lobes of the brain, may contribute to the behavioural impairments in WS. Of course, as Galaburda *et al.* point out, people with SVAS, who have only the elastin gene deleted, should be just as prone to vascular injury, and yet show no signs of visuospatial impairment.

Thus this study provides a tentative link between neuroanatomy and behaviour, and in particular supports the hypothesis that the cognitive profile in WS is related to a deficit in the dorsal stream of visual processing (see section 1.4.1).

Other studies have reported on abnormalities in the cerebellum of patients with WS. Thus Mercuri *et al.* (1997) have identified Chiari 1 malformation in WS (an excess of

cerebellar tissue extending into the upper part of the spinal canal, which can put pressure on the brainstem and spinal cord and lead to neurological symptoms. These researchers also reported abnormalities in the white matter of the brain, involving the centrum semiovale. Reiss *et al.* (2000) have recently carried out a high-resolution MRI study of 14 young adults with WS. They confirmed the reduction in overall brain volume, with a reduction in the size of the occipital lobe, but a relative preservation of the size of the cerebellum. They also found a reduction in the size of the brainstem. Reiss *et al.* (2000) propose that the deletion of the human homologue of the 'frizzled' gene, FZD3 in WS may contribute to this reduction in brainstem volume (but see above for evidence that FZD3 is not necessary for the WS phenotype).

These researchers also found a reduction in the proportion of cerebral white matter, but a preservation in the volume of gray matter relative to controls.

5.1.2. WS and the modularity hypothesis

The uneven cognitive profile in WS has been compared by some researchers with the pattern of deficits found in patients with localised brain damage. Thus the sparing of language abilities coupled with deficits in spatial awareness, alongside a greater ability to reproduce local rather than global elements of a display (Bihrle *et al.* 1989), resembles the pattern of deficits seen in patients with right hemisphere lesions. Similarly, the preservation of face processing, coupled with spatial deficits, is similar to patterns of abilities seen in patients with dorsal-stream damage. Such findings mesh with the view that the adult brain is organised in a modular fashion, where separate brain areas perform discrete functions and localised brain damage can therefore give rise to selective deficits. Whilst the adult neuropsychological literature has provided a wealth of evidence for this view, in the form of double dissociations of function (patient A can perform function X but not function Y, whereas patient B can perform function Y

but not X), the developmental implications of the modularity hypothesis are far from clear.

Certainly, initial speculations that the preservation of language or face recognition abilities in WS represent preserved 'modules' may have to be modified. Thus, even in areas of spared ability, the performance of children with WS is may not be completely unimpaired. For instance, it is known that only a minority of people with WS attain vocabulary appropriate to their age (Mervis *et al.* 1999). Recent studies have also shown that WS children may be using different processing strategies from typically developing children to achieve similar levels of performance. They may also arrive at a similar developmental outcome by different routes. For instance, Karmiloff-Smith *et al.* (1997) report that unlike normal controls, children with WS made more use of featural cues than configural cues in a face recognition test. WS children may also learn their vocabulary in a different way from typically developing children (Stevens and Karmiloff-Smith, 1997). There is also evidence from a study by Paterson *et al.* (1999) that the early levels of performance in a cognitive domain may not predict its developmental outcome, as might be expected if modular functions are innately specified. They report that whilst adolescents with WS score better on language tests than number tests, 2 year old WS children were impaired relative to controls on a language test, but performed better than Downs children and as well as mental age and chronological age matched controls on a numerosity task (preferential looking paradigm used in both tasks).

It may also be the case that where abilities in different cognitive or perceptual domains develop at different rates in the normal case, an imbalance in competence between these domains in WS may simply be a consequence of a delay or a ceiling in

development beyond which WS children do not progress (see discussion of Atkinson *et al.*. 2000b, below).

5.1.3. Ventral-dorsal processing in children with WS

Atkinson *et al.* (1997) tested the proposal that the ventral stream of visual processing may be relatively preserved compared to the dorsal stream, using two pairs of tasks designed to compare dorsal stream function with ventral stream function, the motion and form coherence tasks and the post-box tasks.(see section 1.4.3 for a description of form and motion coherence tests). In the *post-box tasks*, children have to either post a letter into a post-box, or they have to match the orientation of the letter with that of the slot, without actually posting it. Thus the post-box tasks compare the use of vision to control action (a 'dorsal stream' function) with the ability to make a perceptual judgement of orientation (a 'ventral stream' function). Goodale and Milner (1995) have used this task to demonstrate that a patient with ventral stream damage was able to post a hand-held card accurately, but was unable to make an accurate perceptual report of the orientation of the card (see section 1.4.1).

Atkinson *et al.* (1997) found that more children with WS scored outside the normal range on the motion coherence test than on the form coherence test. Similarly, in the post-box tasks, children with WS showed a much greater deficit when posting the card than when matching the orientation of the card to that of the slot. It seems, therefore, that some children with WS have difficulty with tasks which rely heavily on dorsal stream processing. In a later study Atkinson *et al.*(2000b) compared the performance of a larger number of WS children and normal children on the motion and form coherence tests. There was again a group of WS children who show an impairment of dorsal function relative to ventral function. However, many control children between the age of 4-5 years displayed a similar pattern of performance, leading to the

conclusion that in the course of normal development, dorsal stream areas underlying motion coherence performance may develop more slowly than ventral stream areas dealing with form coherence. Thus WS children who perform poorly on the motion relative to form coherence may simply be performing like normal 4 year olds. However, as Atkinson *et al.* point out, WS children who showed poor motion coherence ranged in age from 6-15 years, so their poor performance was unlikely to be due to a delay in development. It is possible that for many WS children, motion coherence perception seems to asymptote at a level equivalent to relatively young children.

The evidence suggests that there may be a deficit in dorsal stream functioning in children with WS. However, it is known that the dorsal stream is not a unitary channel, but consists of a set of functionally and anatomically separate neural pathways. As well as the integration of form from motion in area MT, dorsal stream visual processing areas in the parietal lobe (which receive projections from extra-striate areas including MT), are involved in the processing of grasp-related object attributes (Sakata, 1997). As discussed in chapter 1, there is also evidence for a set of 'parieto-frontal modules' subserving the control of action, involving reciprocal connections between parietal areas and prefrontal areas involved in reaching, grasping, and eye movements (Milner and Goodale, 1995). Consequently it is possible that different aspects of dorsal stream function may be selectively impaired in WS, or may display atypical patterns of co-ordination. The first experiment reported in this section, therefore had two purposes. Firstly, a new test was used to compare ventral and dorsal stream functioning in a different domain - the perceptual and visuomotor estimation of object size. Secondly, kinematic measures were used to study the organisation of the reach and grasp components of prehension in children with WS and typically developing children. By

acquiring data from children across a wide age range, it was also possible to compare the development of this aspect of dorsal stream function in WS with the normal case.

5.1.4. Movement planning in WS

Even if an impairment in dorsal stream functioning is confirmed, this may not fully explain motor deficits in WS. A distinction can be made between two aspects of the planning that go on in the preparation of an object-oriented movement; object based planning, and end-state planning. Object based planning uses information about the immediate properties of the object such as its size, mass, shape and orientation, as well its location relative to the body or other objects – these are the properties thought to be analysed by the dorsal stream. However, a further level of processing is introduced when the intended use or end-state of the object is taken into account. For example, if I pick up a pair of scissors from my desk, I will choose a different grip depending upon whether I am going to pass them to somebody, or use them to cut paper. To choose an appropriate grip in this situation requires the ability to predict what position the object and the limb will be in at the end of the movement. End-state planning is likely to involve the integration of dorsal stream information with pre-frontal areas involved in inhibiting inappropriate actions and co-ordinating the elements of action sequences.

Observation of children with WS when carrying out the post-box task indicates that both object-based and end-state planning may develop atypically in children with WS. Thus, as well as making errors in matching the orientation of the letter to the slot, they also often chose the wrong direction of rotation at the start of the movement, which caused the arm to end up in an awkward position when attempting to post the letter (Atkinson *et al.* 1997). It is possible, therefore that the ability to plan actions efficiently is compromised in children with WS. The second set of experiments reported in this

section test the ability to predict the consequences of action, using two tasks which require a mental rotation of the position of the hand in order to avoid an uncomfortable end-state of the arm.

5.1.5. Aims of this section of the thesis

1. To test the specific hypothesis that spatial and visuomotor deficits seen in WS are due to a deficit in the dorsal stream of visual processing, using different aspects of dorsal stream function than have previously been tested.

2. To chart the development of dorsal stream function/action control in WS and to compare this with typically developing children.

3. To carry out a normative study of action control in typically developing children between 4 and 14 years olds and so to fill a gap in the kinematics literature. This will extend the study of reach kinematics in infants in chapters 3 and 4 through to adolescence.

4. To test the hypothesis that children with WS may have deficits in action control processes thought to be mediated by the frontal lobes.

6 Object based action planning in Williams syndrome.

6.1 INTRODUCTION

In normal adults, the extent to which the hand opens during a reaching movement is finely calibrated to the size of the target object (Jeannerod, 1984). However a number of studies have shown that in patients with damage to the parietal cortex, this calibration is absent or impaired (Jakobsen *et al.* 1991; Goodale *et al.* 1993). Also, damage to both parietal areas and premotor cortex areas in the monkey causes a deficit in grasp formation (Gallese *et al.* 1997). If children with WS have a deficit in dorsal stream object processing, then they should show inaccurate adaptation of the grasp to object size. However, if the dorsal stream is selectively impaired, this should not affect the ability to perform a perceptual estimation of object size.

In order to test for a dissociation between dorsal and ventral stream processing in children with WS, a measure of size estimation that did not involve reaching for the objects was needed. When working with neuropsychological patients, Goodale *et al.* asked subjects to indicate the size of the objects by holding the thumb and forefinger at the appropriate distance apart. However, piloting of this task with children with WS revealed that they found this task difficult to understand. Accordingly, a perceptual size matching task was devised which was easily understood by children. In this experiment, children were first asked to choose from a range of squares the one that

matches a target square. They were then asked to pick up the target square and the width of finger opening was measured using the Elite motion tracking system.

This study also provided the opportunity to carry out a comparative developmental study of the kinematics of the reach and grasp movement in children with WS and typically developing children. Whilst many studies have reported on the organisation of prehension in adults, and also in infants (see chapter 1), few studies have measured the characteristics of prehension in typically developing children between 3 and 15 years.

6.2 METHOD

6.2.1. Subjects

Grasping task: Subjects were 17 children with WS between 5 and 15 years (mean age 9.4 years, sd 2.5 years) and 17 typically developing children between the ages of 3 and 15 years. (mean age 9.1 years, sd 3.2 years).

Size matching task: Subjects were 36 children with WS between 5 and 15 years and 61 typically developing children between the ages of 3 and 15 years.

More children were tested on the size matching task than the grasping task, as the grasping task relied upon the Elite system, whereas the equipment for the size matching task was portable, and so children could be tested away from the lab. In addition, 19 children with WS who did the matching task were excluded for the following reasons: they were disturbed by wearing the markers to the extent that it interfered with the task (6), did not perform the tasks according to instructions (3), or because of data loss (10). (A child was excluded if less than 12/15 trials where both index and thumb markers were visible throughout the reach were available for analysis). 3 control children were excluded because of data loss.

6.2.2. Apparatus.

The apparatus consisted of 3 white squares made from 5 mm thick Perspex, 20mm, 40mm and 60 mm square. A flat reflective marker was placed central to one edge of each block, so that its location could be determined using the Elite system. A series of 7 white squares, with sizes ranging from 10 to 70 mm in 10mm increments, were painted onto blue card to serve as matching templates for the size estimation task. The table upon which the apparatus was placed was also covered in blue card. (see Fig. 6.1)

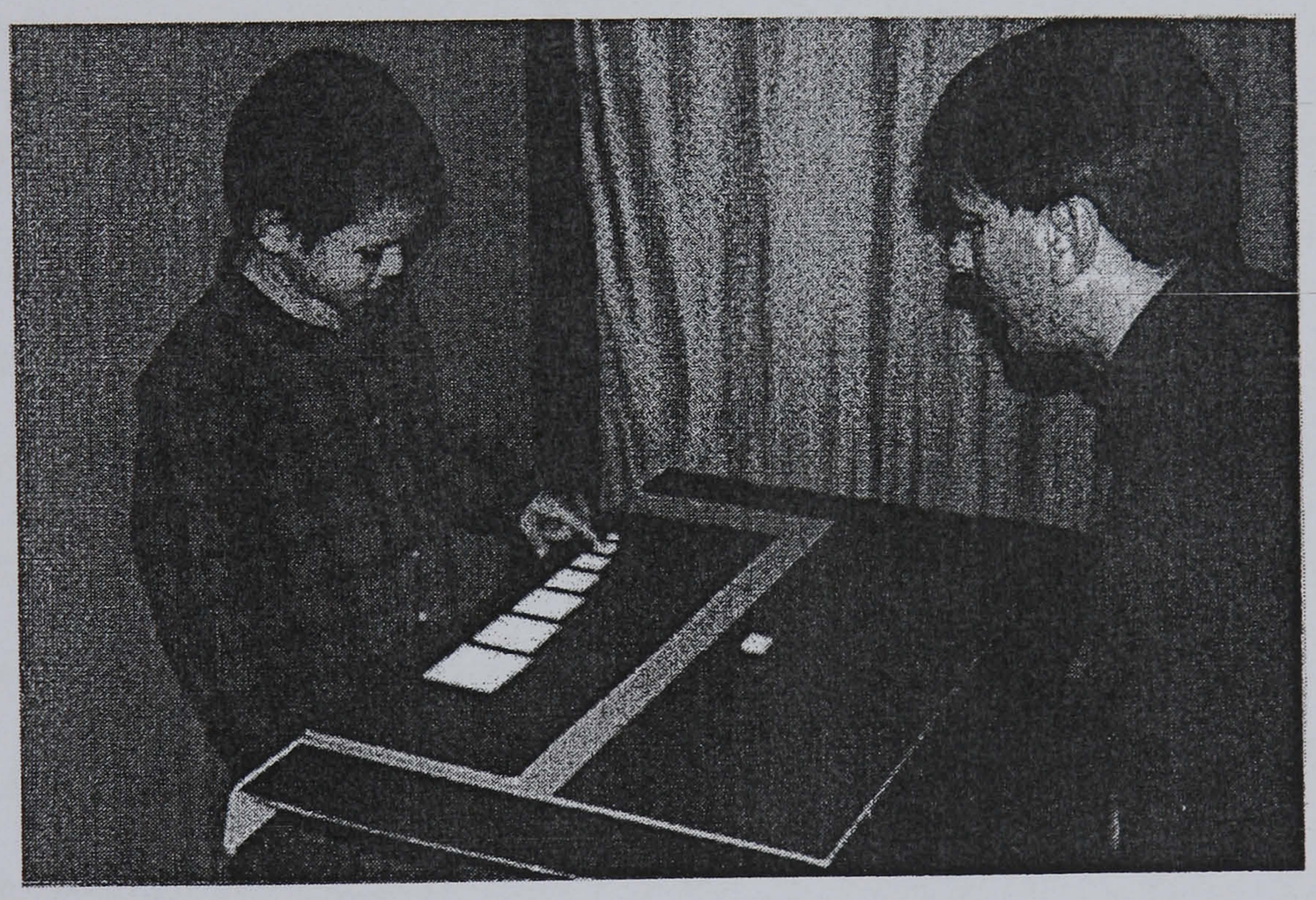


Figure 6.1. Apparatus for the size matching task

6.2.3. Procedure

The order of performance of the perceptual size matching condition and the grasping condition was alternated between subjects.

Perceptual size matching condition: The child was seated at a table of the appropriate height, with the row of white squares placed at the edge of the table, in front of the child. They were then shown the three Perspex squares. The experimenter told the child that he would show them the squares one by one, and that each time their task was to point to the painted square that was the same size as the one the experimenter showed them.

The experimenter placed one of the squares at a point central to the array of squares, 250 mm from the edge of the table. The experimenter pointed to the square and told the child to look very carefully at it. The experimenter then pointed to the array of matching squares and told the child, *"now look at these squares, and point to the one which is just the same size, exactly the same size as this one"*. The child did not receive feedback as to whether they had made a correct choice, but was verbally encouraged throughout testing. Each child was given three practice trials. The three squares were presented five times each, giving 15 experimental trials. Squares were presented in quasi-random order, with the exception that two squares of the same size were never presented consecutively.

Grasping condition: Three reflective markers were attached to the child's hand using hypoallergenic tape. One marker was attached to the index finger, at the base of the finger nail, one to the thumb at the base of the fingernail and one on the back of the wrist.. The child was seated at the table, with the start mark central to the body. The child was told to place their hand at the start mark, with the thumb and index finger together. The experimenter then placed one of the Perspex squares in front of the child, with the nearest edge 250mm from the start mark. A small bowl was placed to the left of the square. The child was told to pick up the square, and to place it in the bowl. (The bowl was used as it was found that younger children found the task easier to understand

if they had to perform a specific task, rather than just picking up the square and putting it down again.) There were again 15 trials, with order of presentation the same as in the size estimation task.

A number of dependent variables were calculated from the kinematic record for each trial. Variables describing the grasp component were the peak distance between the finger and thumb markers (*maximum aperture*) as well as the *percent time taken to reach maximum aperture*. Variables relating to the reach component were *movement duration, maximum hand speed, number of peaks* in the hand speed profile, *deceleration time* (percent time after maximum hand speed) a *straightness index,* and a measure of *maximum deviation.* Maximum deviation was calculated as the maximum deviation of the hand path from a straight line connecting the start and end point of the reach.

6.3 RESULTS

6.3.1. Correlation between object size and grip size

Correlations between object size and peak aperture are presented in Figure 6.2 All typically developing children showed a significant correlation between peak aperture and object size. However, three children with WS show a very poor, and statistically non-significant, adaptation of grip size to object size. These children tended to open the fingers to the same size regardless of object size. Figures 6.3a and 6.3b show peak aperture for each of the three objects for one WS child with poor grasp adaptation and a typically developing child of the same age who shows good grasp adaptation.

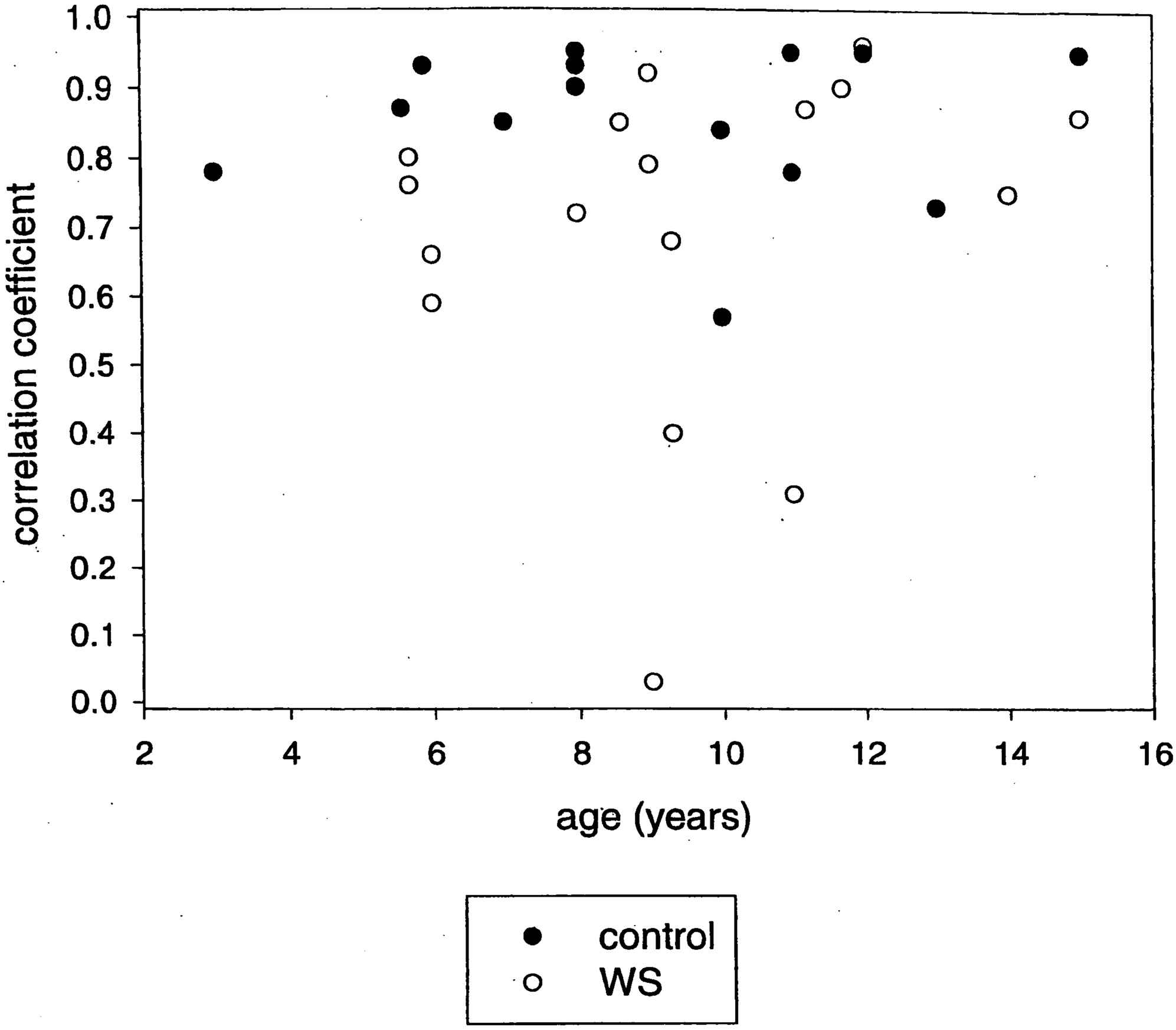


Figure 6.2 Correlations between object size and maximum grip aperture

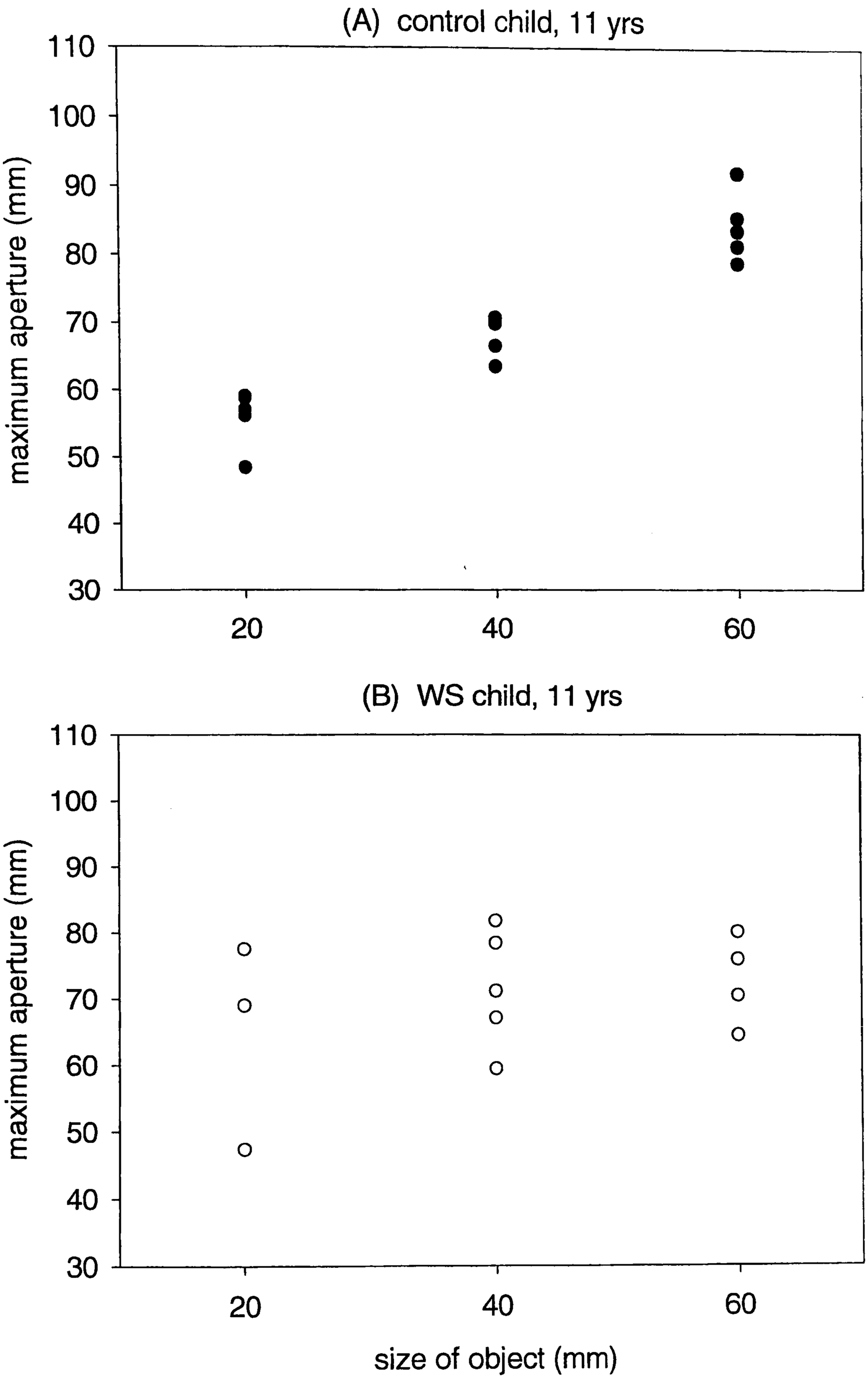


Figure 6.3 Maximum grip aperture whilst grasping objects of three different sizes.
(a) CNO:11 year old typically developing child
(b) LBU: 11 year old WS child

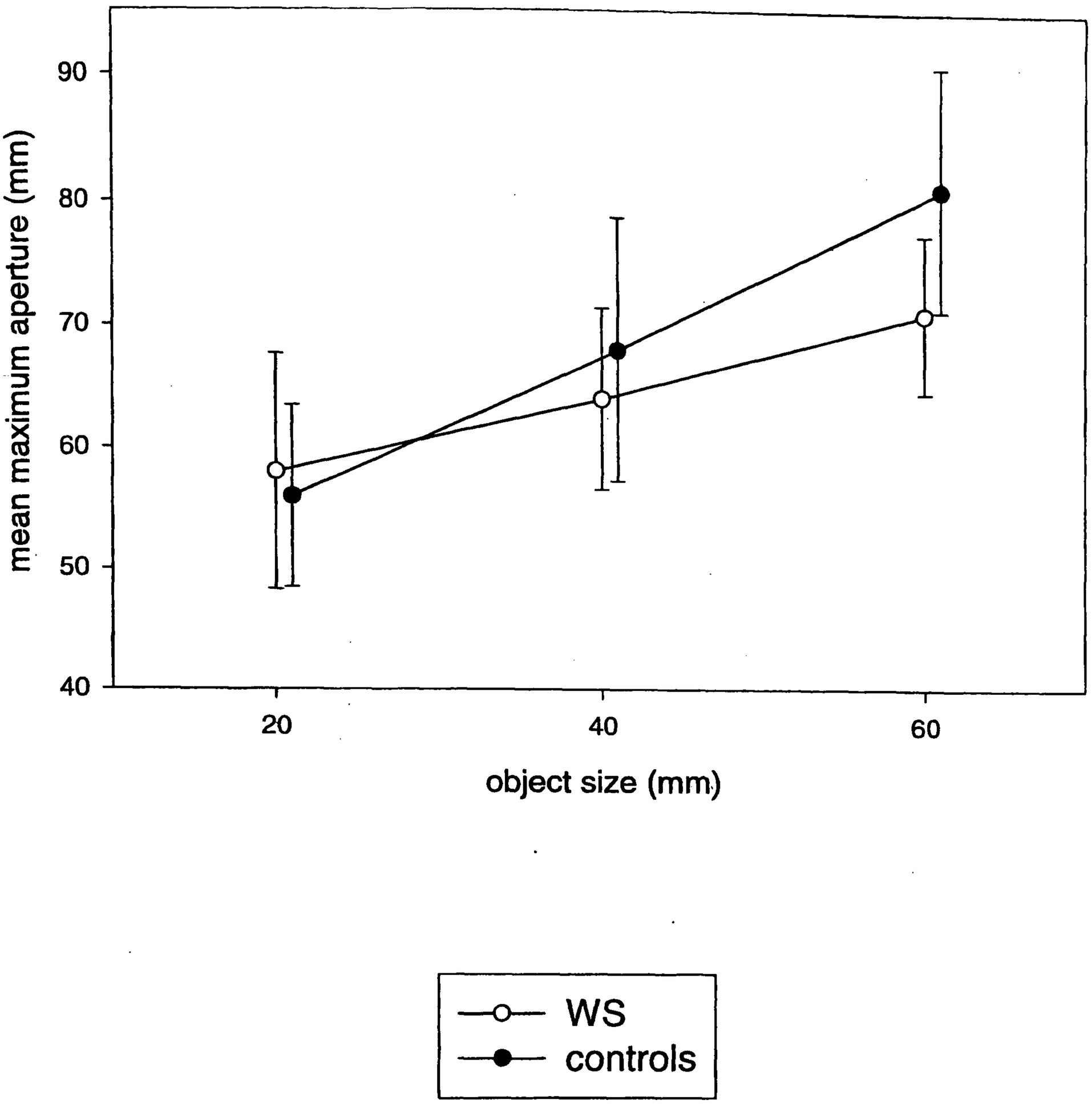


Figure 6.4 Mean maximum grip aperture for each object size.
Error bars are plus or minus 1 standard deviation.

Figure 6.4 shows the mean maximum grip aperture for each of the objects. A 2x2 mixed model ANOVA with object size and group as independent variables was used to test for differences between groups in the adaptation of the grip to object size. There was a main effect of object size, $F(2, 58) = 183.25$; $p<0.001$. there was no effect of group, but the interaction between object size and group was significant, $F(2,58) = 15.74$; $p<0.001$. A number of points are apparent from Fig. 6.4. Mean maximum aperture is very similar in both groups for the smallest (20mm) object and both groups show a linear increase in aperture with increasing object size. However, children with WS make smaller increases in maximum aperture as object size increases. Thus the mean change in grip aperture for a 20 mm increase in object size is 7 mm for children with WS, whereas it is 12 mm for control children. Also, the standard deviations of maximum grip size reached for each object are smaller on average for WS children than for control children. So whilst changes in maximum grip size may be less well matched to changes in the size of the object in children with WS, individual grasps to a given object size are nevertheless quite consistent. (One possible explanation for the differences between groups would be if WS children made smaller adjustments to object size because their hands are smaller on average than control children. If this were the case, mean change in maximum aperture between objects of adjacent sizes should be greater in older than younger children, as hand size increased with age. In order to test this possibility, the correlation was calculated between mean change in grip size and the age of the subject. This correlation ($r = 0.3$) was not significant.)

As stereo vision may be an important factor in the programming of the reach and grasp movement, the stereo vision status of each child with WS was measured and is also presented in table 6.1.

Table 6.1. Correlations between object size and maximum grip aperture in WS children

subject	Grip/object correlation	age	stereo status
Cfr	0.96**	12	240
Wes	0.83**	14	Neg
Nra	0.86**	15	Neg
Tri	0.92**	9	240
Jco	0.59*	6	240
Dre	0.66*	6	Neg
Lbu	0.31 ns	11	240
Hre	0.79**	9	240
Fre	0.03 ns	9	1200
Tor	0.72**	8	550
Jbe	0.9**	11.7	240
Swa	0.87**	11.2	240
Tgu	0.68**	9.3	240
Lmg	0.8**	5.7	Not tested
Jsh	0.61*	5.7	Neg
Ban	0.4 ns	9.3	Neg
Kbu	0.85**	8.6	120

** p<0.01; *p<0.05
stereoacuity measured using TNO test: neg = no stereopsis. Numbers are TNO stereoacuity in seconds of arc. Lower values indicate greater stereoacuity.

6.3.2 Perceptual size matching.

Scores on the size matching task (number of trials with a correct match) are presented as a function of age in Figure 6.5. and table 6.2. In order to ascertain whether errors on the task were due to a systematic bias in perception, a measure of constant error was also calculated by taking the mean (signed) difference in size between the chosen square and the target square. A measure of whether the subject's choice was more than one square away in the series from the target square is also presented in Table 6.2.

Whilst control children over 6 years are matching correctly on all trials, almost all WS children except one make errors on the task. In addition, no control children misjudged the size of the square by more than 1 cm, whereas errors of this magnitude

were common in children with WS. There is some indication that performance improves with age in children with WS, but that this improvement is considerably delayed compared to control children. Despite the large difference in mean score between the groups, constant error is similar for each group. There is therefore no evidence from this measure of a systematic bias in WS size perception.

Table 6.2. Scores on size matching task (children who did reaching task)

	group	
	control	WS
Mean score/15 (sd)	13.0 (3.2)	5.7 (4.1)
Mean constant error	-0.8	0.7
No. of subjects making errors larger than 1 cm.	0	8

6.3.3. Results of size matching from larger sample

In order to compare perceptual size matching ability in WS children and typically developing children, the test was given to a larger sample of control children and results compared with those from all 37 WS children who performed the task. From Table 6.3 it can be seen that errors made by WS children are again greater in magnitude than those made by controls, and levels of constant error are similar. Fig. 6.6. shows that in control children there is a sharp increase in the ability to perform the size matching task around 6 years, with 2/22 children over 7 years scoring 12 or more on the test. Children with WS have much greater difficulty with the test, with 19/20 WS children over 7 years scoring less than 12 on the test. Regressions predicting size match score from the chronological age of the subjects were significant for both control and WS children, (WS children, $F(1,34 = 10.2$; $p<0.002$, R-sq = 0.23); control children $F(1,60 = 18.58$; $p<0.001$, R-sq = 0.23). In order to test whether performance was related to a measure of (verbal) mental age rather than chronological age, a regression was also calculated using

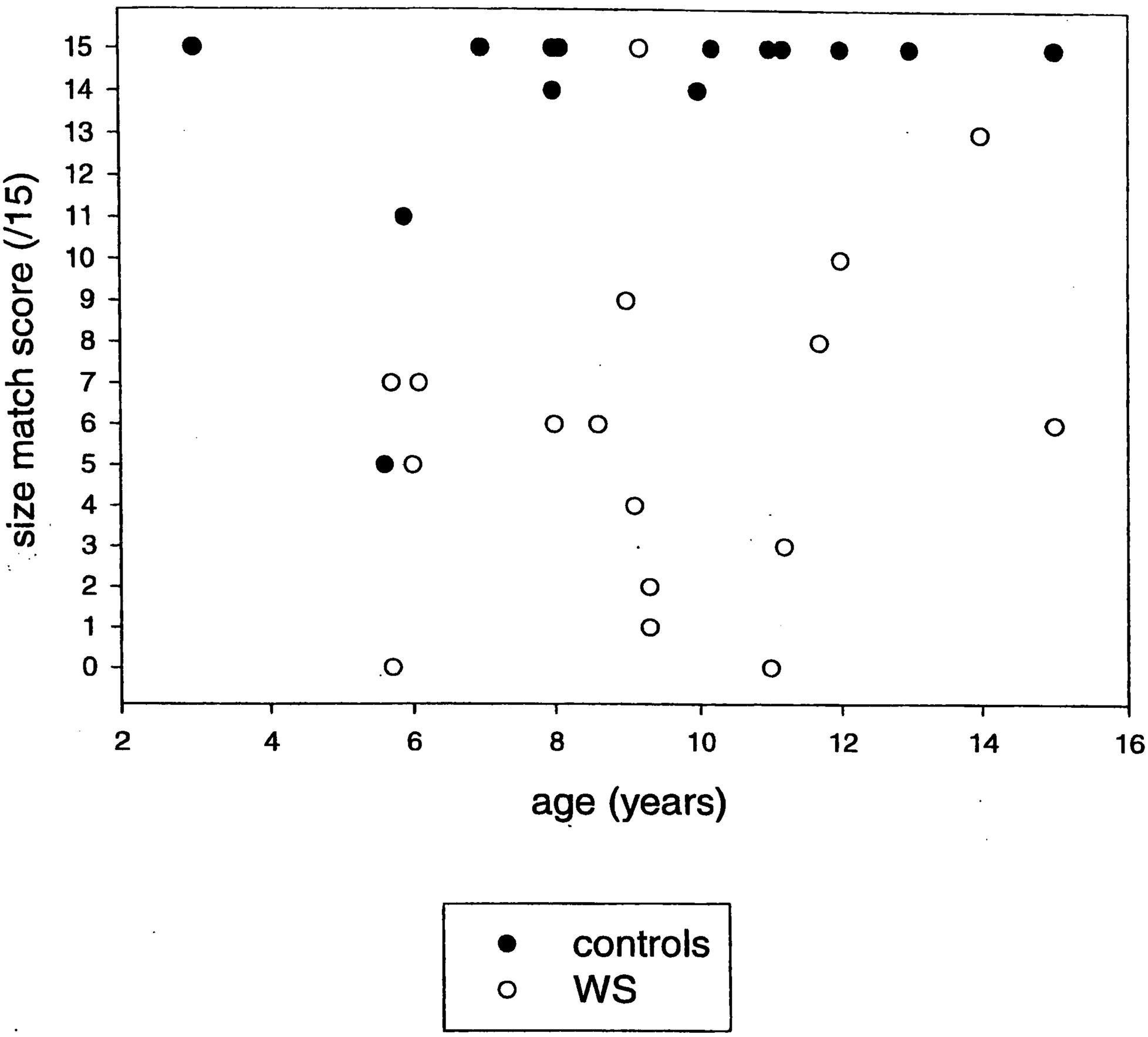


Figure 6.5 Scores on the size matching test

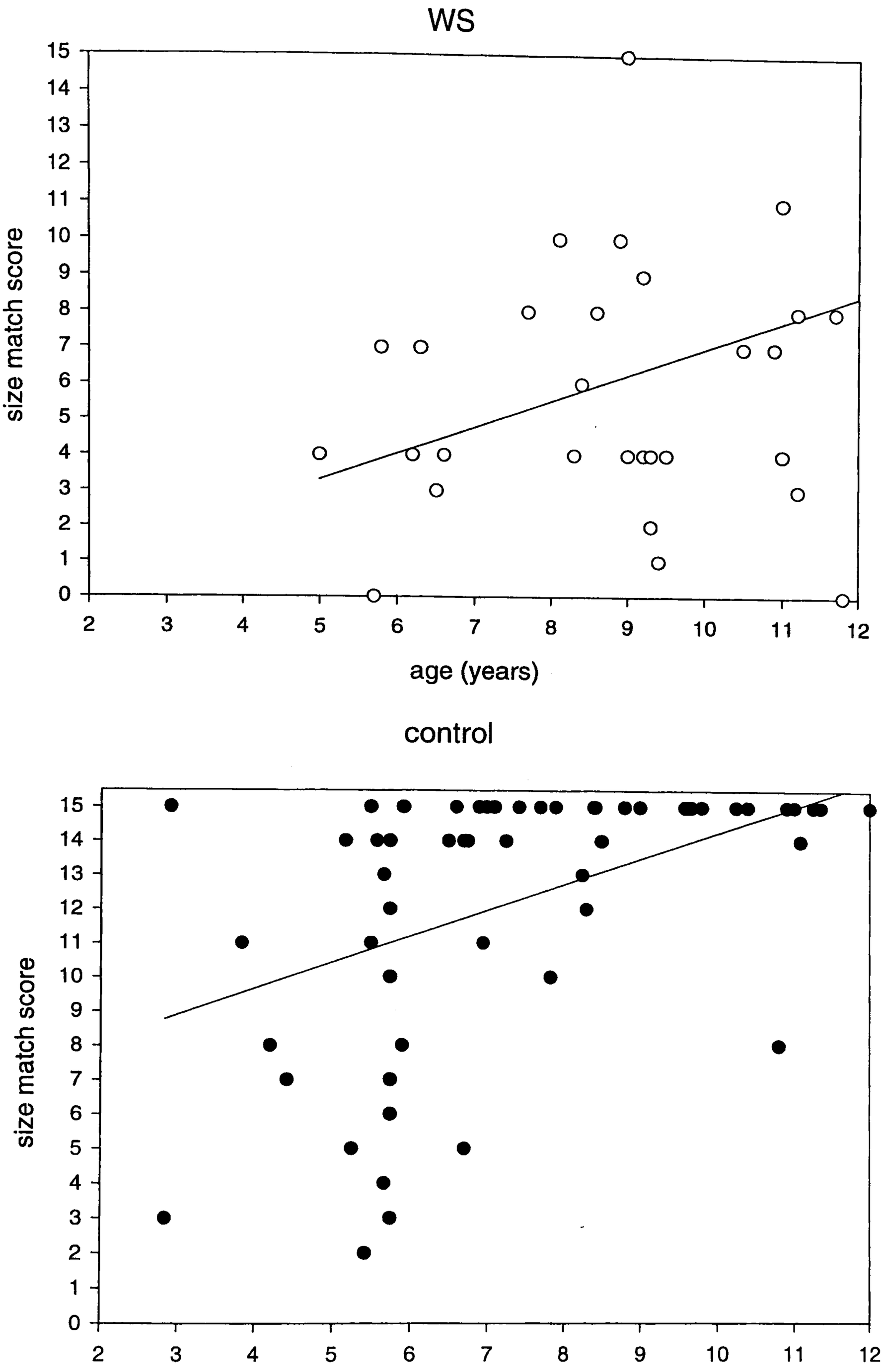


Figure 6.6 Size match scores from larger sample.
Regression lines are superimposed

the age equivalent on the British Picture Vocabulary Scale (Dunn *et al.* 1982) as the predictor for the WS children's scores. This regression was not significant. If the regression equations based on chronological age are used to calculate the predicted age at which a perfect score would be achieved, this is 20.64 years for WS children, and 11 years for control children. Thus, whilst there is evidence of age-related improvement in WS children, this is significantly delayed compared to control children and performance may never reach the level of older controls in some WS children.

(regression equations: WS children score = -0.48 + 0.75 age

control children score = 6.86 + 0.74 age).

Note : A linear model may not be the best fit. However the preceding analysis gives some indication that there is development of this ability in WS children during childhood.)

Table 6.3. Scores on size estimation task (all children)

	group	
	control	WS
Score	12.5 (2.4)	6.4 (9.1)
Mean constant error	-0.68	-0.9
No. of subjects making at least 1 error larger than 1 cm.	2/61	15/36

6.3.4. Comparison of perceptual size matching and grip scaling.

Figure 6.7 shows a comparison of size matching scores and grip correlations for individual children for whom data is available on both tasks. It is clear that children with WS tend to score worse than controls on both measures. In addition, there is only one child who shows impairment on the 'dorsal' grip scaling measure relative to the ventral' perceptual size matching measure. With the exception of this one child, there

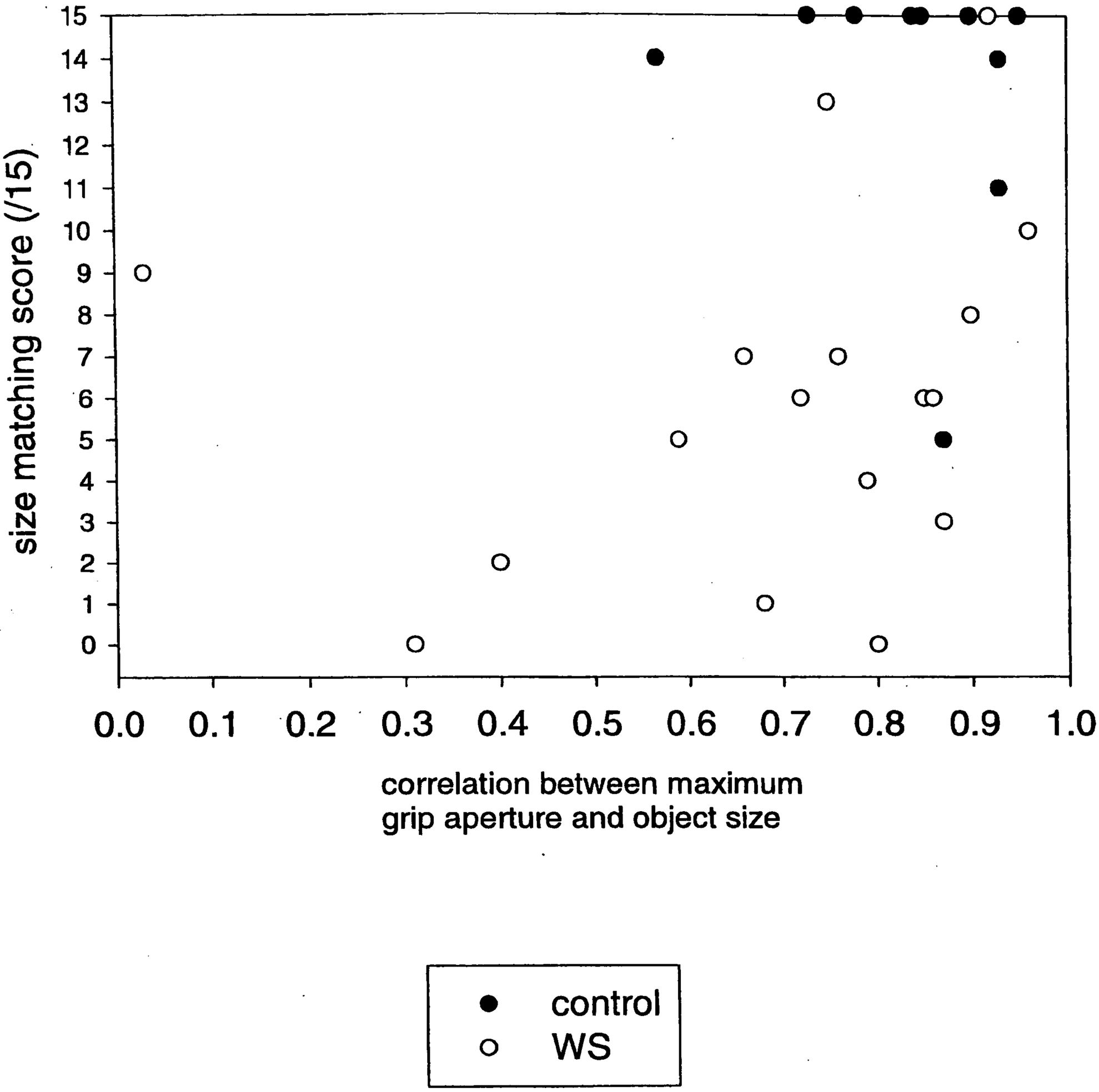


Figure 6.7 Comparison of size matching and grip scaling
Size matching score is plotted as a function of the correlation between object size an dmaximum aperture.

also seems to be an association between scores on the two tasks in children with WS. *(If this 'outlier' score is left out the correlation between the two measures is significant).*

6.3.5 Comparison with shape matching test from ABCDEFV.

It is interesting to compare the results of the size matching task with another test carried out (on a different set of children) in the Visual Development Unit. In the shape matching element of the Atkinson Battery of Child Development Examining Functional Vision (ABCDEFV; Atkinson, 1989), children are presented with a board, from which 5 distinctively shaped holes have been cut - a star, triangle, square, circle and rectangle. On each trial, a wooden shape which matches one of the holes is given to the child, who is asked to place it in the correct hole. On this test, 4/5 is marked as a pass. 75% of 2 year old control children passed the test, (n = 142), and 99% of 3½ year old controls (n = 129). Of 12 WS children over 3 years old who did this test in the VDU, 11 passed, (three 3yr old Williams did the test, all passed) and two out of five 2 year old Williams children passed the test. Thus, it seems that Williams children over 3 years perform as well as controls on this match-to-sample shape perception task.

6.4. DISCUSSION

This experiment set out to test the hypothesis that children with WS have a particular difficulty with tasks that rely upon dorsal stream processing, as opposed to ventral stream processing. However, Williams children performed worse than controls on both 'ventral' and 'dorsal' tasks. Thus, although kinematic measures showed that children with WS may have subtle deficits in dorsal stream function, children with WS seemed to also show difficulty with making accurate judgements about object size and shape, tasks which are thought to be mediated by the ventral stream of visual

processing. Only one child showed the pattern of performance that would be expected of a subject with an impairment of the dorsal stream relative to the ventral stream of visual processing. This result seems at odds with those from the post-box task, another task designed to dissociate ventral and dorsal stream processing. Atkinson *et al.* (1997) found that a majority of children with WS scored within the normal range in the 'ventral' aspect of the post-box task – the matching of the letter's orientation to that of the slot. Why should children with WS be less successful at the size matching task? One possible explanation is that the orientation matching element of the post-box task may be simpler than the size matching task used here, in that it only requires a one–to-one match of letter to slot. In the size matching task, children were required to choose one square from a range of squares of different sizes. However, young WS children seemed to be quite successful at a match-to-sample task involving different shapes, as in the ABCDEFV. It is also possible that the post-box task is more embedded in a practical context, in that rather than having to understand a concept like 'same size', the child is told to 'set the letter so the man can post it'. Similarly, children with WS score very low on the Benton line test, which requires two lines of the correct orientation to be selected from an array of 11 and yet perform relatively successfully on the matching element of the post-box task. This may again due to differences in the level of abstraction in the two tasks. One could test this possibility by creating a motor version of the size matching task, in which rather than pointing to the correct match, the child is asked to place it into a square well of the correct size.

It should also be noted that a significant minority (5/11) of the subjects in the Atkinson *et al.* study showed an impairment relative to normal 4 year olds on the matching task. As Atkinson (2000) suggests, children with WS may exhibit a 'persisting global immaturity' in visual processing, with the high performance on face

recognition tasks representing a special case of preserved ventral stream function. The data from this experiment support this view. Thus, whereas the performance of both groups on the size estimation task improves with age, control children show a rapid improvement between the ages of 5 and 7 years, and most score perfectly on the task after this age. The equivalent period of improvement is greatly extended in children with WS, and all the WS adolescents still make mistakes on the task. It is interesting that a statistical relationship was found between the chronological age of WS children and their performance on this task, but a similar relationship was not evident when BPV age was used as the predictor.

6.4.1. Adaptation of grip size to object size in WS.

Mean maximum aperture is very similar in both groups for the smallest (20mm) object and both groups show a linear increase in aperture with increasing object size. However, children with WS make smaller increases in maximum aperture as object size increases. The similarity in maximum aperture for the 20mm object may be a 'floor effect' in that the apertures observed for this object may be close to the minimum possible, given that the markers were fixed on the outside of the finger and thumb. The lower maximum apertures for the other two objects observed in children with WS are interesting because other studies have shown that a reduction in the amount of visual information available during the reach gives rise to an *increase* in mean maximum aperture (e.g. Jakobsen and Goodale 1991; Berthier *et al.* 1996). Adults seem to adopt a default larger aperture to cope with the uncertainty caused by the lack of visual information. Similarly, Haggard *et al.* (1994) report on a patient with a right cerebellar lesion, who when grasping a dowel opened the affected hand much wider with than the unaffected hand. Haggard *et al.* propose that this is a strategic compensation for a lack of proprioceptive information about the current position of the hand when grasping,

caused by the cerebellar lesion. Thus, it is unlikely that the differences in grip size between WS children and controls are due to a degradation of visual or proprioceptive feedback.

The standard deviations of maximum grip size for each object are also lower on average for WS children than for control children (see Fig. 6.4). So whilst changes in maximum grip size may be less well matched to changes in the size of the object in children with WS, individual grasps to a given object size are nevertheless quite consistent. This would seem to indicate that there is a systematic bias rather than a global inaccuracy in grip scaling in children with WS. Perceptual size matching measures indicate that this bias does not affect comparisons of object size, although of course any perceptual bias is likely to operate in the perception of both the target object and the array of matching squares. Another possibility is that the bias lies in the transformation of information about object size within the dorsal stream, perhaps in distance-scaling mechanisms. Servos *et al.* (1992) have demonstrated that grasping movements made under monocular conditions show lower peak apertures than under binocular conditions. In addition, monocular reaches were longer in duration, had lower peak velocities and a longer proportion of the reach was spent in deceleration (see the discussion of other kinematic parameters below). They argue that subjects were underestimating the distance, and consequently the size, of the target object when reaching with one eye covered. Is this a feasible explanation of WS children's performance? Certainly, some of the children with WS have deficits in stereo vision, which might be expected to cause errors in distance estimation. However, there is no clear relationship between stereo status and accuracy of grip scaling (see table 6.1)

6.5 COMPARISON OF REACH KINEMATICS FOR CHILDREN WITH WS AND TYPICALLY DEVELOPING CHILDREN.

Whilst many studies have reported on the organisation of prehension in adults, and also in infants (see chapter 1), few studies have measured the characteristics of prehension in typically developing children between 3 and 15 years. An exception is Pryde, Roy and Campbell, 1998, who compared kinematics of the reach in children age 9-10 years and adults, reaching for three different sized cubes. Children were found to spend more time in deceleration than adults, and peak aperture was reached at a later point in the reach. When grasping smaller objects, both children and adults spent longer in deceleration and maximum aperture was reached at an earlier point in the movement. The aim of this analysis was to compare the kinematics and temporal organisation of the reach and grasp components of prehension, in children with WS and typically developing children. In addition, this analysis fills a gap in the literature, by completing the picture of how the kinematics of the reach develop between early childhood and adolescence. Kinematic parameters of the reach were therefore calculated for the grasping movements reported above.

6.5.1. Subjects for reach analysis.

Subjects were the same children as for the analysis reported above, except that wrist marker data was available for the three control children whose data was excluded from the grasp analysis because of occlusion of finger markers.

6.5.2. Results of reach analysis

Means and standard deviations of kinematic variables describing the reach are presented in Table 6.4 for children with WS and typically developing children.

Table 6.4 Means and standard deviations of kinematic variables

	WS		Controls	
Measure	**mean**	**sd**	**mean**	**sd**
Duration (ms)	**1010.00**	220.39	**760.01**	70.03
Number of peaks	**1.66**	0.52	**1.08**	0.13
Maximum hand speed (ms/sec)	**643.83**	112.13	**732.71**	121.26
Straightness index	**1.12**	0.06	**1.19**	0.12
Maximum deviation (mm)	**34.97**	23.60	**52.54**	23.86
Time to maximum aperture (ms)	**600.33**	200.98	**490.86**	80.73
Percent time after maximum hand speed (deceleration time)	**59.97**	6.09	**55.68**	4.60
Percent time to maximum aperture	**63.91**	13.01	**65.64**	7.15

Movement duration.

Mean movement duration was longer for WS children than controls. Figure 6.8 shows the mean movement duration for WS children and controls, as a function of age. It is apparent that movement time was longer for WS children than control children for children throughout the age range, with two younger WS children moving particularly slowly. An independent t-test showed a significant difference between means; $t(32) = -4.02$, $p<0.001$. Linear regressions were calculated to test for age trends in the data. The regression for WS children approached significance.

Maximum hand speed.

Maximum hand speed was higher for control children than WS children (see Fig. 6.9) An independent t-test showed a significant difference between means; $t(32) = -2.15$, $p<0.04$

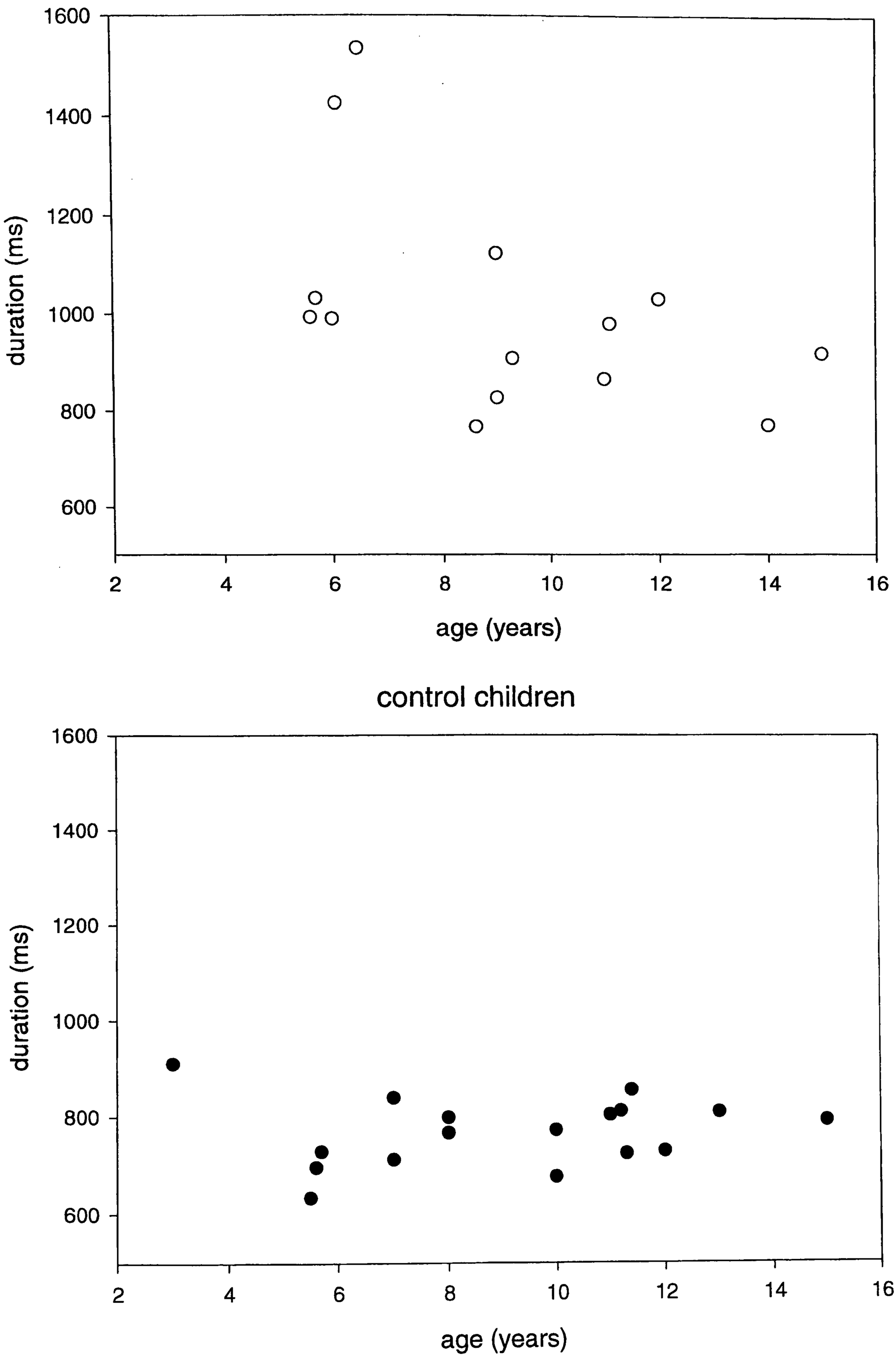


Figure 6.8 Mean duration of reach

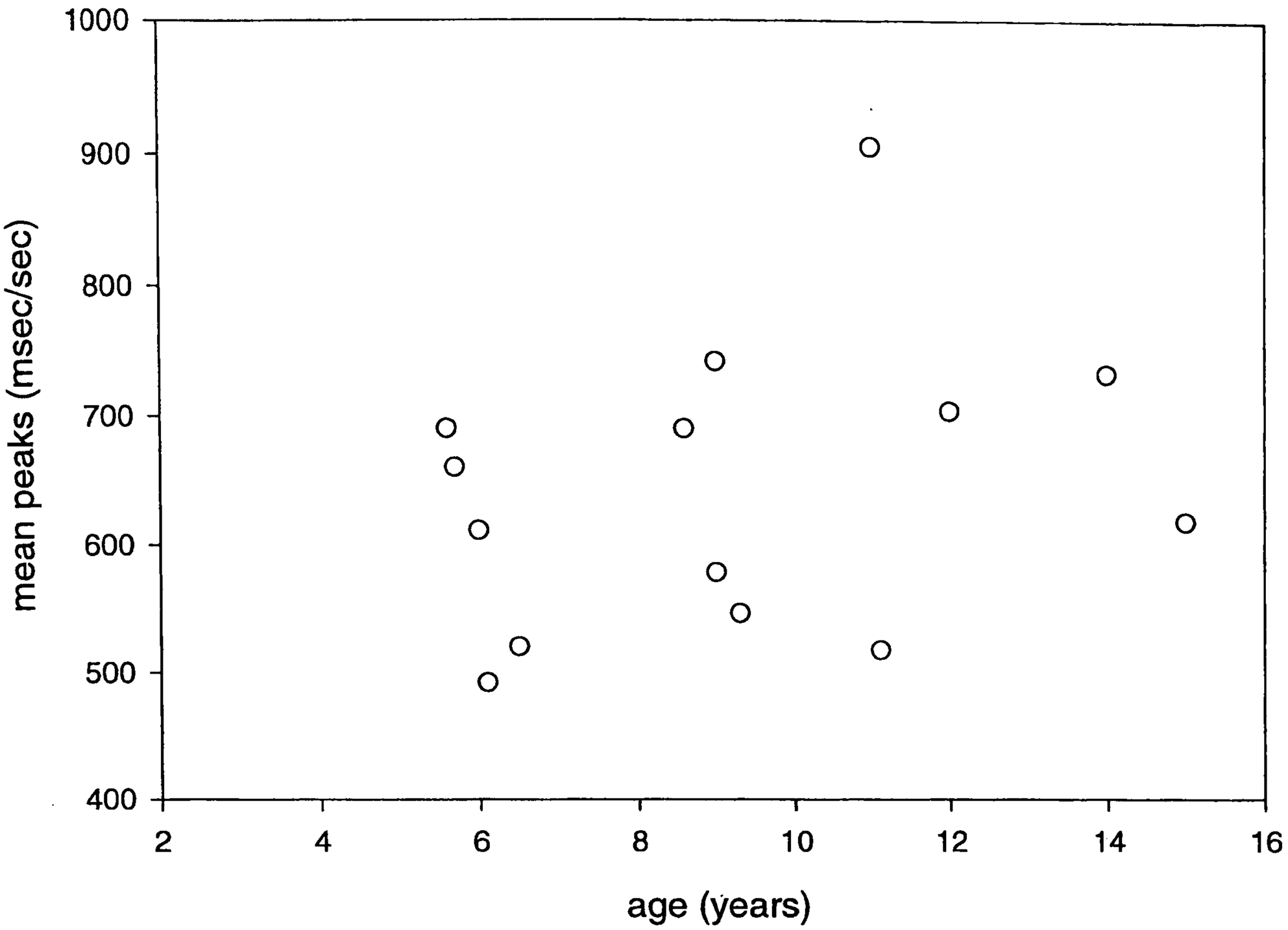


Figure 6.9 Mean peak hand speed

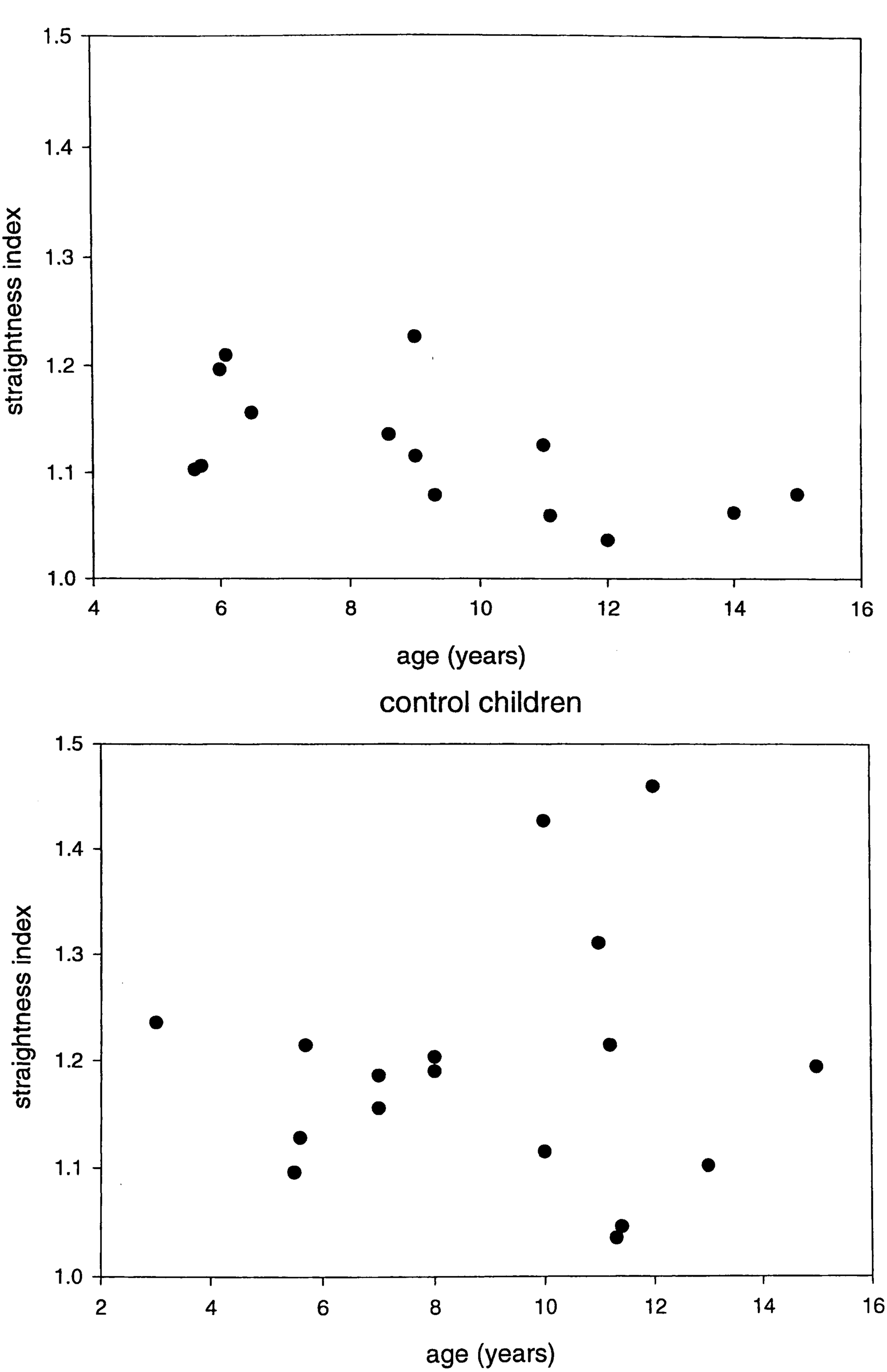
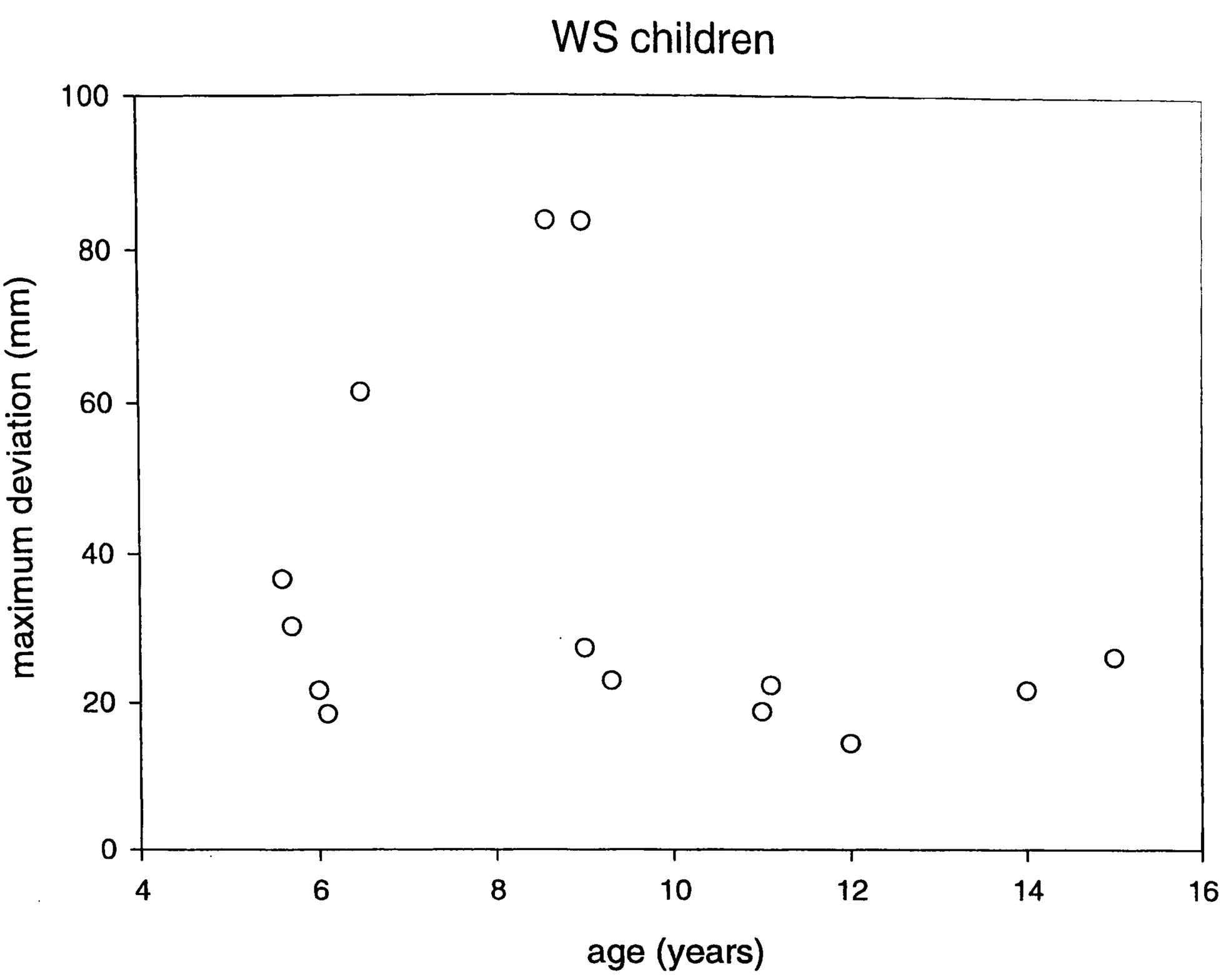


Figure 6.10 Mean straightness index
(where an index of 1 indicates a perfectly straight reach)



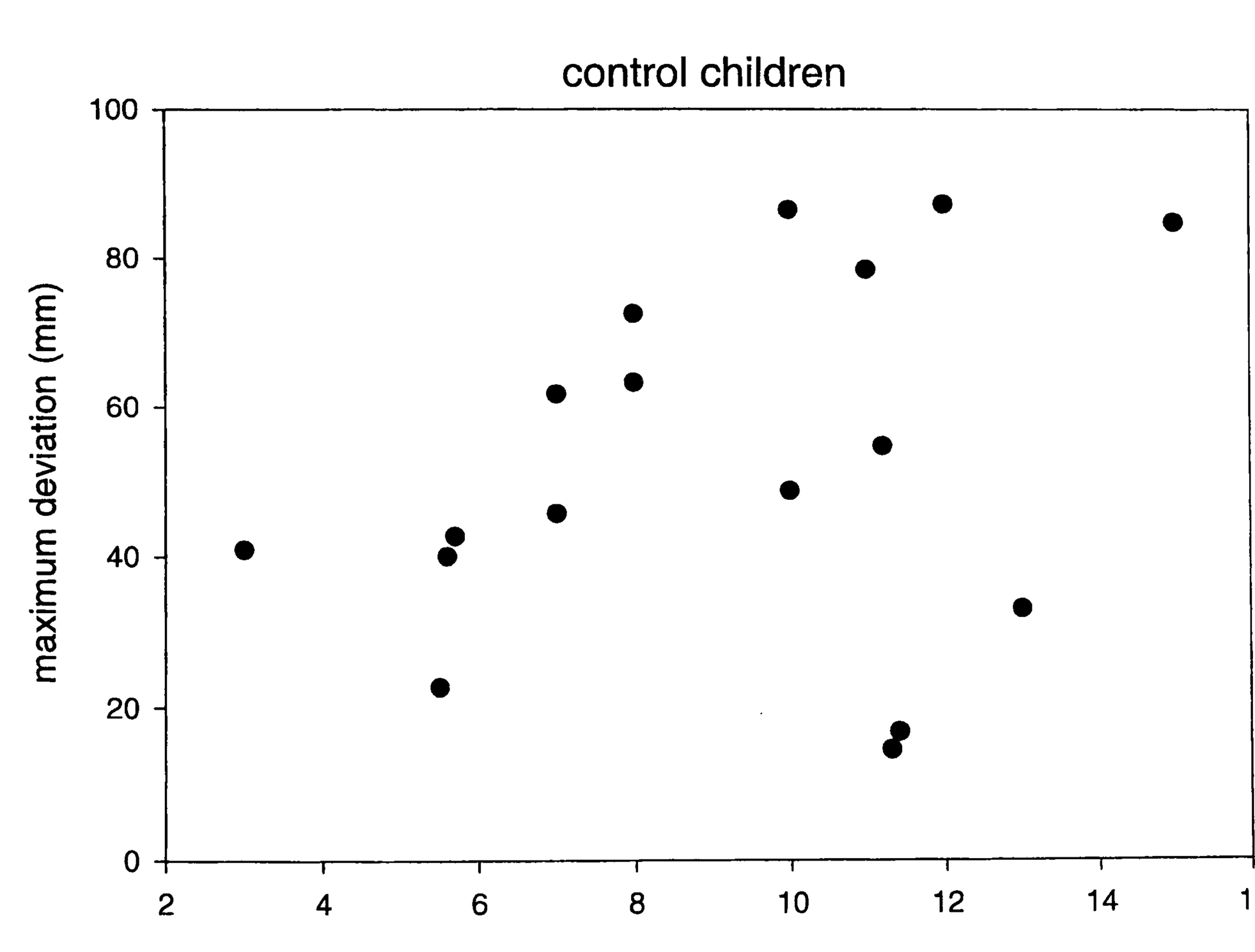


Figure 6.11 Mean maximum deviation of the reach (Maximum deviation from a straight line connecting start and end point of the reach)

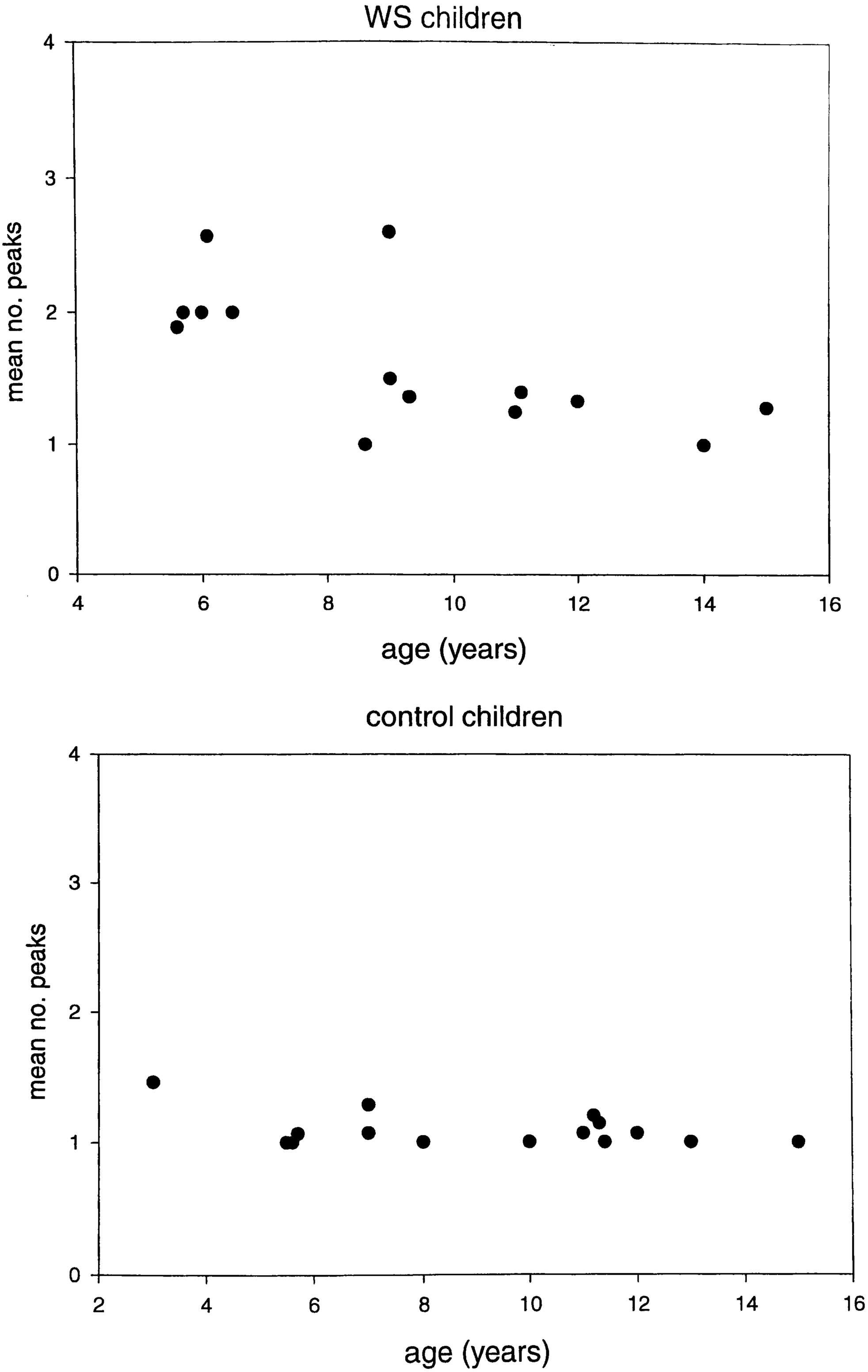


Figure 6.12 Mean number of peaks in hand speed profile

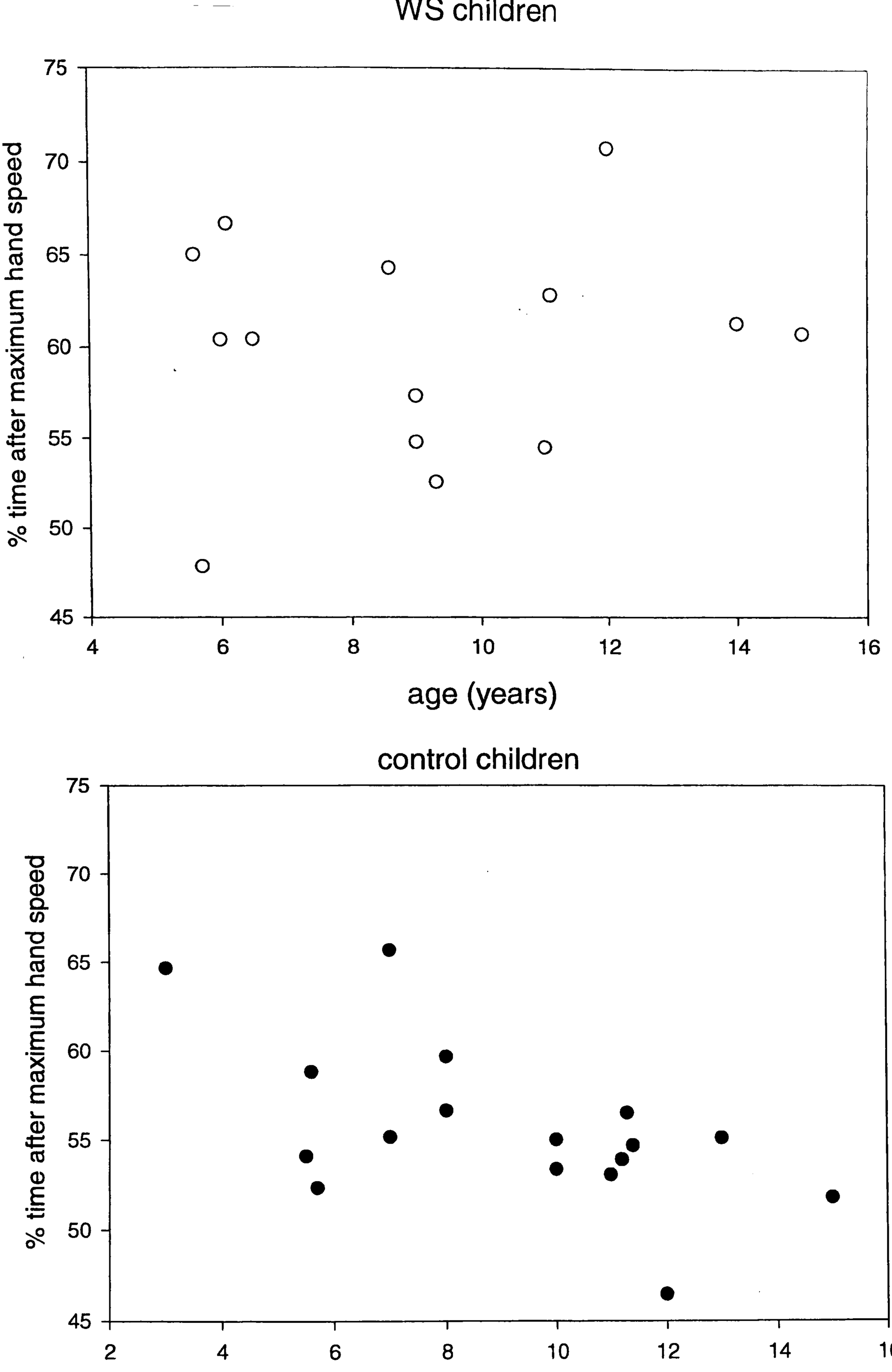


Figure 6.13 Mean percentage of reach duration spent in deceleration (Percentage time after maximum hand speed attained)

Straightness index

The straightness index of reaches made by WS children was lower than that of control children, indicating there was less variability in the trajectory of WS children's reaches. (see Fig. 6.10) Differences between the groups were statistically significant $t(32) = -2.2$, $p<0.04$.

Deviation.

The maximum deviation of WS children's reaches was also lower than in control children (see Fig. 6.11). Differences between the groups were statistically significant $t(32) = -2.66$, $p<0.01$.

Number of peaks.

From Figure 6.12 it can be seen that typically developing children showed a higher proportion of single peak reaches than children with WS. Figure 6. 13 shows the mean number of peaks in the movement for WS children and controls. From this figure it can be seen that whereas for the majority of control children the mean number of peaks is close to one, younger WS children show a larger mean number of peaks in their movements. Independent t-test showed a statistical difference between the groups; $t(32) = -4.3$, $p<0.001$ Regression analysis was used to investigate whether older children with WS showed less peaks in hand speed profile than younger children. The slope of the regression was negative and significant ($y = 2.7x - 0.11b$; RSq = 0.45), $F(1,15 = 12.4)$ $p<0.003$, indicating that the number of velocity peaks in the movement decreased with age in children with WS. A similar regression performed on control children's data was not significant.

Percent time spent in deceleration.

Children with WS spent a larger proportion of the reach in deceleration than control children ($t(32) = -2.38$, $p<0.02$) (see Fig. 6.13). Regression analysis was used to

investigate the relationship between age and deceleration time. For control children, the slope of the regression was negative and significant ($y = 63x - 0.8b$; RSq = 0.34), F(1,16 = 7.9) $p<0.01$, indicating that the proportion of the reach spent in deceleration decreased with age in control children. A similar regression performed on WS children's data was not significant. Figure 6.13 shows the percent time spent in deceleration plotted as a function of age.

Percent time to maximum aperture

Control children and WS children spent a similar proportion of the movement reaching maximum aperture. T-tests revealed no significant difference between means (*or standard deviations)* for this variable. This indicates that the temporal organisation of the reach and grasp components is similar in the two groups.

6.6 DISCUSSION: COMPARISON OF REACH MEASURES

Comparison of reach measures shows that reaching movements made by children with WS and typically developing children differed in a number of ways. They took longer overall, and had a lower maximum velocity. They also spent a larger proportion of the reach in deceleration. However, straightness and deviation measures indicated that WS children's reaches were more direct than those of control children. It is possible that this reflects more developed end-state planning of the reach in the control children, as because of the layout of the apparatus, control children may have curved the trajectory of the reaches in order to anticipate the movement required to place the square in the bowl. Despite the decreased variability in trajectory, WS children showed more 'movement units' in the hand speed profile. However, the

relative timing of the reach and grasp components of the movement were similar for the two groups.

Taken together, these results suggest that children with WS are controlling their reaches differently from control children: the increased duration and lower speed, coupled with the increase in time spent in deceleration suggests that the reach is less automaticised, perhaps making greater use of online feedback control. Evidence from adult studies suggests that the deceleration phase is the portion of the reach where visual feedback is used to make adjustments in trajectory. This suggestion is supported by the greater number of movement units in WS reaches. Movement units may reflect the tendency to divide the reach into smaller sub-units, rather than programming the whole of the reach in advance (Brooks, 1974). WS children may be doing this because they are less able to scale the reach to the correct distance. In this case it might be adaptive to undershoot and then home in on the object with a series of smaller sub-movements. Another possibility is that motor output is more unpredictable in children with WS and therefore an optimal strategy is to minimise variability in the output by splitting the reach into smaller sub-segments. This explanation has been used to explain the tendency for infants' reaches to be multi-peaked. (Berthier, 1996).

Children with WS show no developmental trend in the proportion of the reach spent in deceleration whereas control children show a decrease in the time spent in deceleration with age. The control result is consisted with the result of Pryde, Roy and Campbell (1998), who showed that 9-10 year old children spent longer in deceleration than adults. From the results of Pryde *et al.* (1998) and the present study it can be inferred that there is a slow developmental decrease in the proportion of the reach spent in deceleration throughout childhood. In the light of this result, it may be the case that children with WS show no developmental trend in this parameter because even the

oldest children with WS have not reached the level of motor maturity at which significant decreases in deceleration time occur. The data from this study suggest that the transition to using single-peaked movements, which takes place in the first 3 years of life in normal development, takes much longer in children with WS. Even the youngest control children in this study tended to use reaching movements that have a bell-shaped velocity profile with a single velocity peak. Similarly, Konczak *et al.* (1997) have shown that the majority of reaches made by typically developing children at the age of 2½ years consist of one movement unit. By contrast, the decrease with age in the number of movement units in children with WS suggests that the ability to program reaching movements as one unit is developing throughout middle childhood in WS, which represents a significant delay when compared to the typical course of development.

Overall, the results of the comparison between WS and control children of kinematic measures describing the reach suggest that whilst, like typically developing children, they were successfully reaching out, grasping the object and placing it in the bowl on every trial, they were using different control strategies to attain the same goal. Two pieces of evidence support the view that children with WS have a problem with accurately scaling the reach for the distance of the object. Firstly, grip size seems to be under-scaled with respect to object size in WS children, suggesting that they are underestimating the distance and therefore the size of the objects. Secondly, there are a greater number of velocity peaks in the movements made by WS children than controls, despite the fact that their movements were on average straighter. This suggests that mid-reach corrections are made to compensate for an inability to accurately scale the reach to the distance of the object. This finding may help to explain why children with

WS have difficulty in walking downstairs, or on uneven surfaces. When descending stairs, the whole weight of the body must be thrown behind an aimed movement of the foot and leg and there is little room for correction once the movement has started. In addition, the consequences of inaccuracy are considerably greater than in a reaching movement.

The results of this analysis also indicate that there is a continuing immaturity in WS in the dorsal stream units controlling reach and grasp. The reduced velocity, extended deceleration phase and greater number of movement units seen in reaches made by children with WS, is also seen in ataxic patients (Jakobsen *et al.* 1991), and in infants as they are first learning to adapt their reaches to the properties of the object (see chapter 3). This may indicate that these groups are less able to rely upon the rapid, automatic and accurate guidance of movement provided by the dorsal stream of visual processing

This study also indicates that even in the normal case, there is a slow process of refinement in the reach and grasp movement throughout childhood, despite the fact that this movement may be repeated hundreds of times a day.

7 End state planning of action in Williams syndrome.

7.1 BACKGROUND: VISUOSPATIAL AND VISUOMOTOR ABILITIES IN WS.

Children with WS reach motor milestones later than typically developing children, they are often delayed in learning to walk and in the development of fine motor skills and on a standardised test of motor function (Motor ABC) they show an average delay of at least 2 years (Atkinson *et al.* 1996; Henderson and Sugden,1992). Problems that persist into later life include uncertainty when negotiating stairs or uneven surfaces, (Atkinson *et al.* 1996; Dilts, Morris and Leonard, 1990), awkward gait and joint contractures in some children, (Kaplan *et al.* 1989) and difficulty with the use of tools such as spreading or cutting with a knife (Dilts, Morris and Leonard, 1990).

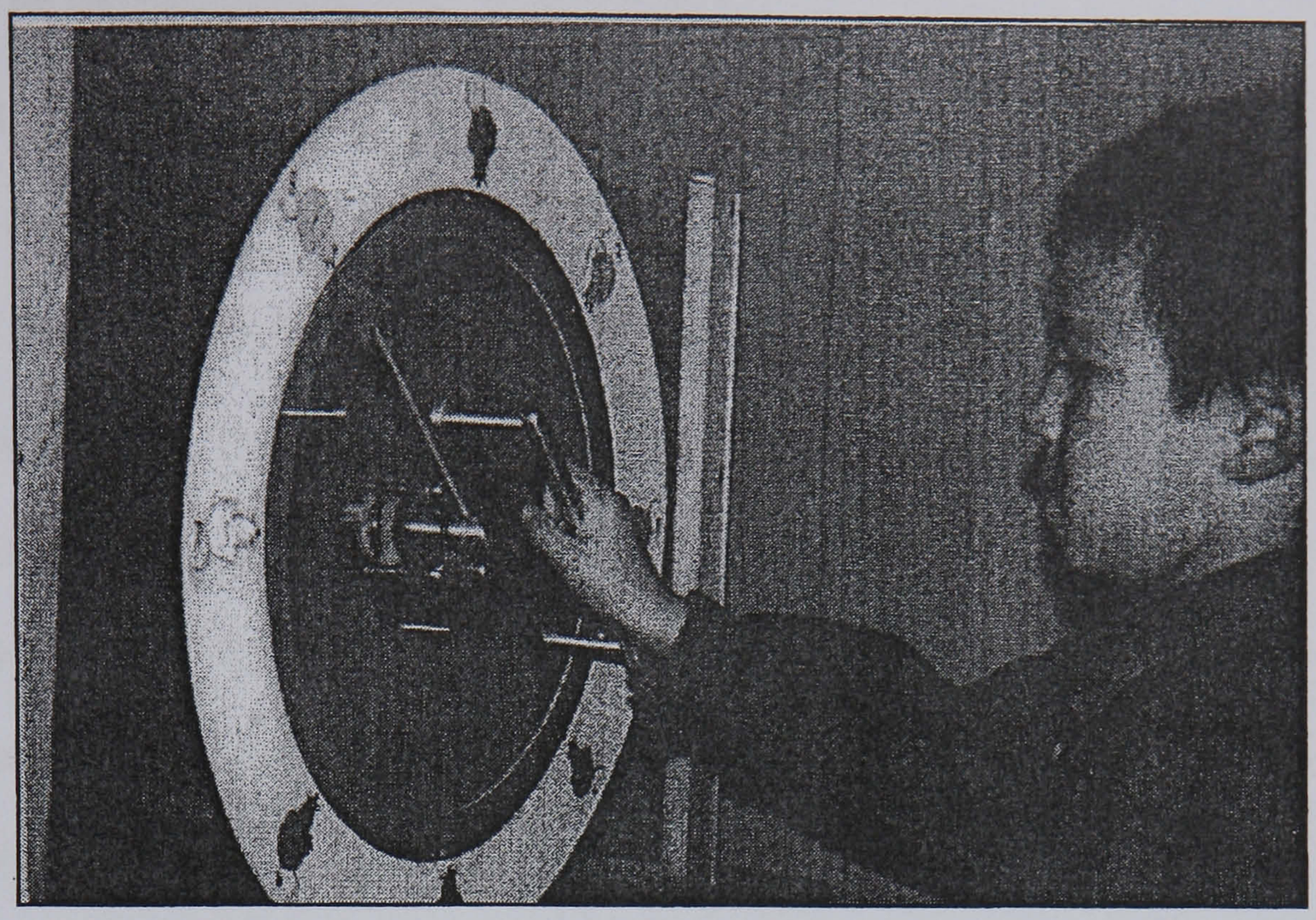
Children with WS also experience problems with visuospatial tasks. They have a poor short term memory for spatial information (Jarrold *et al.* 1999). Their drawings are disorganised and show a failure to synthesize the elements of object being drawn into a coherent whole. They also show problems in copying spatial arrangements of blocks ((block design subtest of WISC-R) and hierarchically organised displays, in which a larger shape is made up of smaller shapes (see Bellugi Sabo and Vaid, 1988, and Atkinson *et al.* 2000a). However, a characteristic feature of children with WS is a greater ability to reproduce local rather than global elements of a display (Bihrle *et al.* 1989).

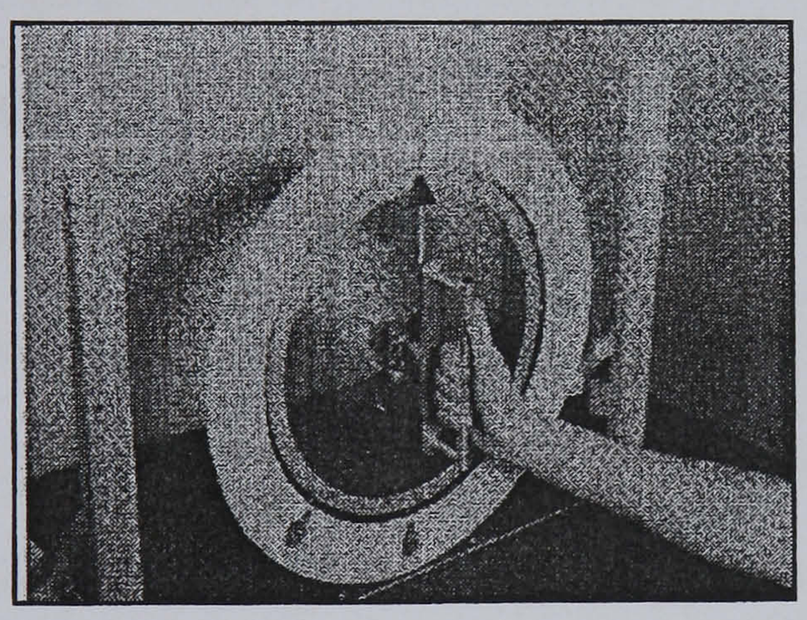
In addition, children with WS score very poorly on the Benton Line test, which involves matching the orientation of two simultaneously displayed line segments to an array of lines of different orientations, and also on tasks which involve mental spatial transformations (Bellugi *et al.* 1988). Atkinson *et al.* (1997) reported that when WS children were doing the post-box task they seemed to have problems planning how to carry out the posting action. They would often, for instance, end up with their hands in very awkward positions because they had rotated the card in the wrong direction to start with. This supports the view that children with WS have a particular problem with using visual spatial information to control action. Indeed, perhaps the most basic application of skills such as spatial transformations and orientation matching is in the planning and organization of one's own actions. Despite this fact, relatively little attention has been paid to how children with WS translate visual information about objects and their spatial arrangements into motor commands. Accordingly, this study set out to test the relation between visuomotor transformation and movement planning using a task which requires a mental rotation of the position of the hand in order to avoid an uncomfortable end-state of the arm.

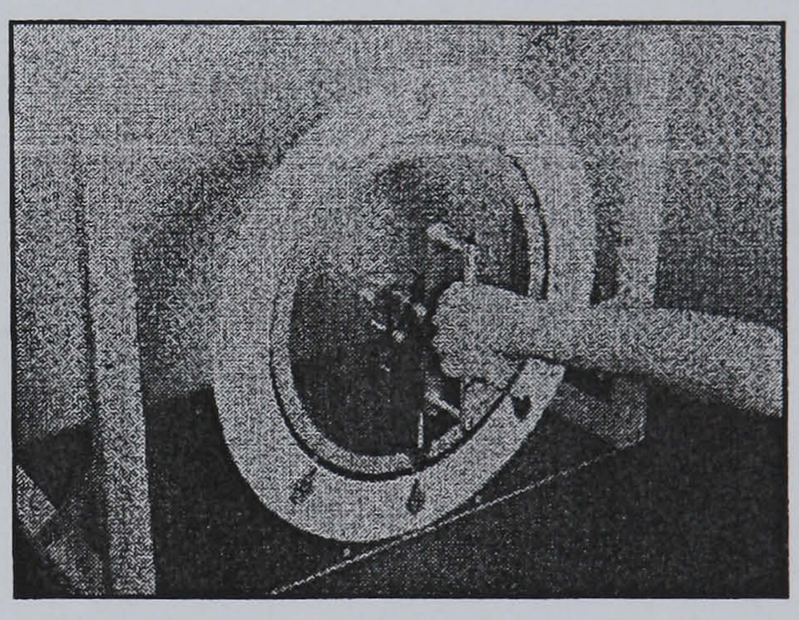
Two tasks were adapted from a study of movement planning in normal adults by Rosenbaum *et al.* (1992). In the Handle Rotation task subjects are asked to grip and turn a handle through 180 degrees to point to a coloured mouse on a large dial (see Fig. 1). In the Bar Task, children are asked to pick up a wooden bar, and to put the end of it into a coloured hole (see Fig. 2). Both tasks test end-state planning - the ability to choose a grip that avoids an awkward hand position at the end of the movement.

7.2 THE HANDLE ROTATION TASK.

From Fig. 7.1 it can be seen that if you are asked to turn the handle round through 180 degrees from a vertical position, and you start with your thumb pointing upwards (a), after a certain point the arm will get close to the limit of its range of rotation, and will end up in quite an uncomfortable position (b). However, you can avoid this by turning the hand over at the start of the movement and grabbing the handle with the thumb pointing downwards. Then when the handle reaches the desired position the arm is in a comfortable state, near to the centre of its range of rotation. Rosenbaum *et al.* (1992) have shown that adult subjects tend to behave in this way - trading off discomfort at the start of the movement for comfort at the end of the movement. What are the advantages of planning for end-state comfort? One possibility is that fine positional control is easier to achieve if the hand is in a comfortable position. Empirical support for this explanation has been provided by Short and Cauraugh (1999), who showed that adult subjects were more likely to use a grip which lead to end-state comfort if the accuracy demands of the task were increased by making the target smaller. There may also be biomechanical factors that contribute to the end-state comfort effect. By moving from the uncomfortable to the comfortable position, the force deriving from the unwinding of the tension of the muscles in the arm is exerted in the direction of the movement. Rosenbaum *et al.* also showed that a tendency to plan for end-state comfort was not the only influence on subjects' choice of grip. Subjects were also more likely to grasp the handle with the thumb and forefinger towards the 'pointing end' of the handle. Rosenbaum has dubbed this tendency the *thumb-towards bias*. They believe that the reason for this bias is that attention in manual tasks is usually focused around the thumb and forefinger and that this part of the hand is therefore more likely to be associated with the 'pointing end' of the handle.







(a.) (b.)

Figure 7.1 Apparatus for the handle task.

7.2.1. The development of end-state planning

Rosenbaum *et al.* (1992) propose two possible explanations for the way adult subjects deal with the handle task. They can compute, for each trial, the grip which will lead to a comfortable end-state, effectively treating each trial as a fresh event. Alternatively, they can remember for each target position which is the most efficient starting position of the hand, and then retrieve this position from memory when that target position is indicated. Whilst the computation method is more flexible in situations where unexpected task demands are likely, the memory method is fast and efficient in predictable situations. Rosenbaum's data support the memory model, implying that subjects retrieve efficient postures from memory rather than recomputing the best grip on each trial. Smyth and Mason (1997), using a similar task, have shown that typically developing children show an increase in the proportion of 'end-state comfort' grips between 6 and 8 years of age, as do children with Developmental Co-ordination Disorder (DCD). They propose that the development of rapid and automatic movement planning may involve building up a memory store of candidate postures. This depends upon successful solutions being found in early life, by the computation method, to everyday movement planning problems similar to those posed by the handle and bar tasks. Difficulties with visuo-spatial transformations like those reported in WS may lead to children finding less adaptive solutions to motor planning problems, which may have consequences for the development of fluency and automaticity in movement in later life. The major aim of this experiment therefore, was to compare developmental changes in movement planning in children with WS and a group of typically developing children.

7.2.2. Movement strategies

When comparing the development of movement planning in children with WS and typically developing children, one can also ask what strategies children use before they reliably plan for end-state comfort. If subjects are consistent in their grip choices during the experiment, there are four possible strategies available when approaching this task (see Fig. 7.2). It should be noted that in the version of the task used in this experiment, children were only asked to turn the handle to target positions at or near the top and bottom of the dial)

1. Stereotypical strategy

The first strategy is simply to raise the hand and grasp the handle on every trial with the thumb facing upwards. This strategy has the lowest cost - in terms of comfort and movement complexity, at the beginning of the movement, but the highest cost at the end of the movement as it never leads to a comfortable position.

2. Thumb-towards strategy.

The second strategy is to always grip the handle with the thumb towards the arrow. This strategy might be used if the subject is planning the grasp using information about the *immediate* properties of the object to be grasped, but not the future position of the object. Attention in manual tasks is usually focused around the thumb and forefinger, so it is quite a good plan to bring together the part of the hand associated with pointing and fine motor control with the 'pointing end ' of the handle. The problem with this strategy is that is only partially successful in this task – only on 50% of trials does it lead to a comfortable end position.

3. Thumb away strategy

The third strategy would be to always grasp the handle with the thumb away from the arrow. This strategy is a logical possibility, but has no practical advantages.

4. Planned strategy

The fourth strategy is to think ahead, and choose the grip that leads to a comfortable position at the end of the movement. By following this strategy, the hand will always end up in the comfortable thumb-up position as the arrow is brought to the target.

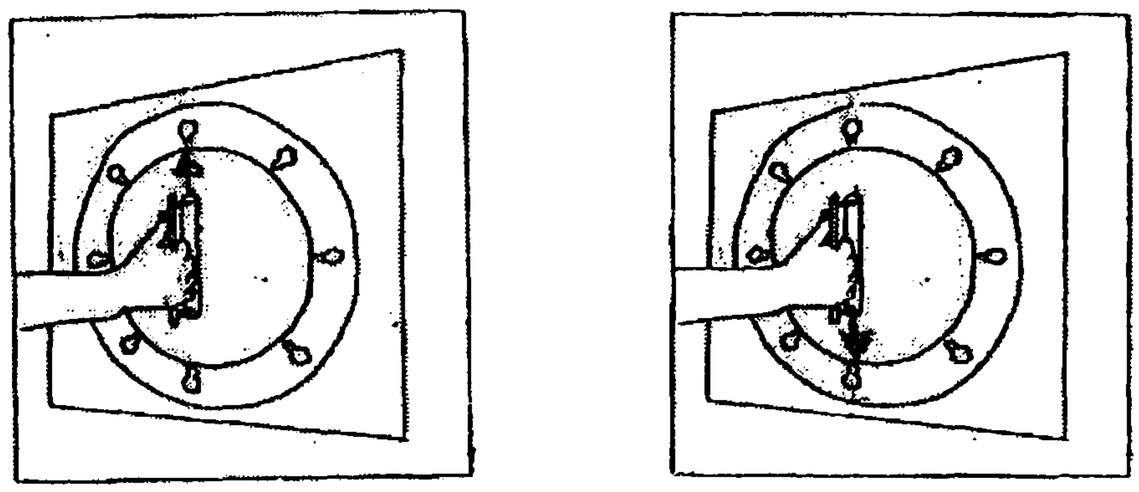
Smyth and Mason's data show that children between 4 and 5 years (both 'clumsy' children and typically developing controls) show the thumb-towards bias before they are reliably planning for end-state comfort. A suitable analysis of the grip choices made by children in this experiment will show whether children with WS and typically developing children are using the same strategies, even when they are not planning for end-state comfort

7.3 METHOD

7.3.1. Design

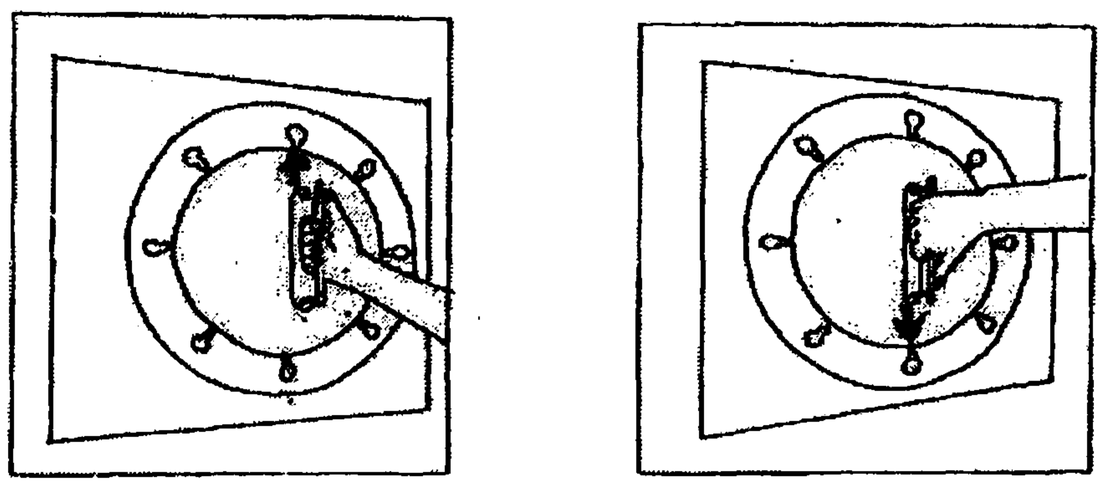
The experiment tested the effect of target position upon grip selection. This effect was compared for children of different ages in both experimental groups (WS or control). Four target positions were used, two at the top of the dial (positions 1 and 8) and two at the bottom of the dial (positions 4 and 5). The dependent variables were the proportion of grips made with the thumb towards the arrow at each position and the proportion of 'end-state comfort' grips. (An end state comfort grip for target positions at the top of the dial would be with thumb towards the arrow, whereas an end-state

1



1. Stereotypical - always grasp with thumb upwards on every trial

2



2. Thumb-towards - always grasp with thumb towards the arrow

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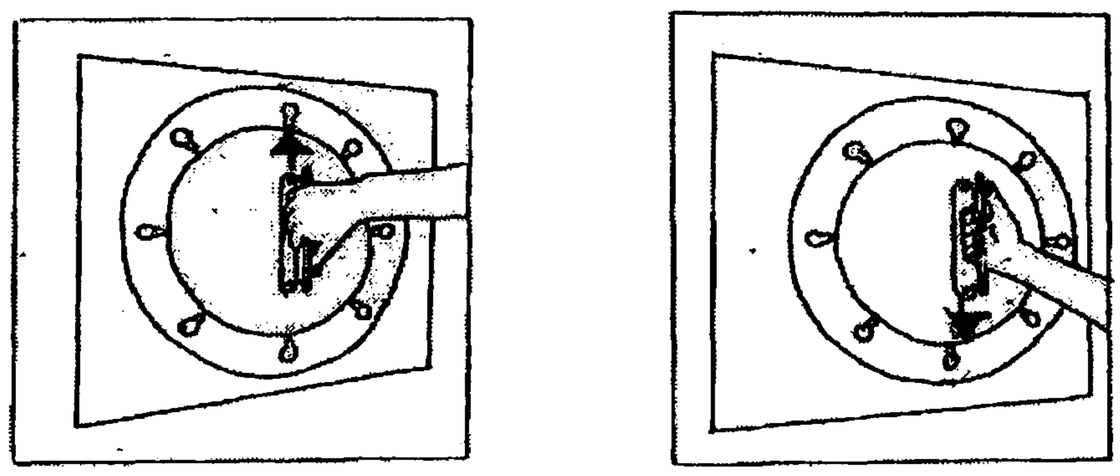
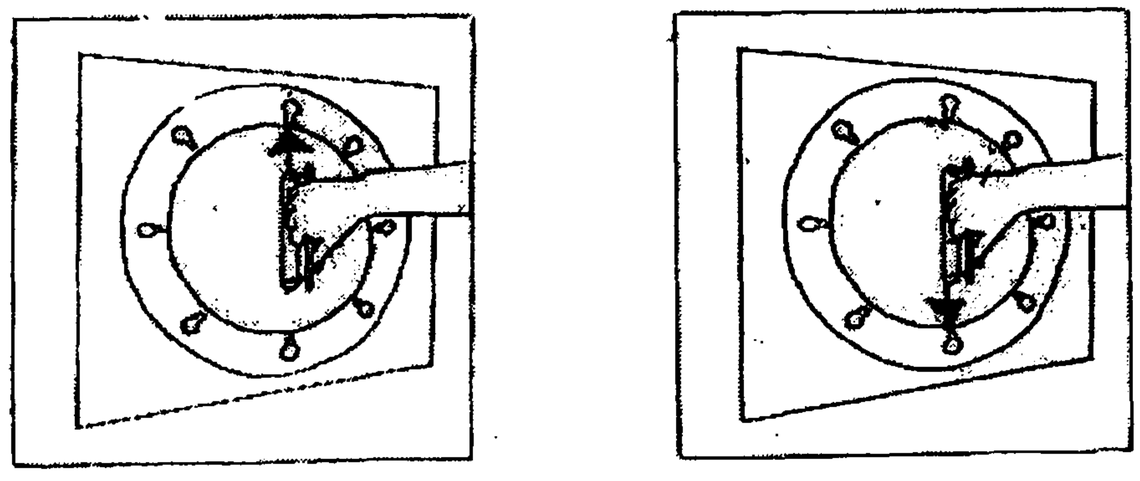


3. **Thumb-away** - always grasp with thumb towards the arrow

4



4. Planned - always choose grasp that leads to end-state comfort.

Figure 7.2 Movement strategies for the handle task. See text for details

comfort grip for target positions at the bottom of the dial would be with the thumb away from the arrow, see Smyth and Mason (1997) for a similar analysis).

7.3.2. Participants

Participants were 37 children with Williams syndrome, between the ages of 5 and 14 years, and 40 typically developing children, between the ages of 4 and 11 years.

7.3.3. Apparatus and procedure

The handle rotation apparatus consisted of a Perspex sheet, 7mm thick, upon which was mounted a circular cardboard dial, 320mm internal diameter, with eight positions marked at equidistant points around the circumference. A picture of a mouse was placed at each of the eight positions on the dial, with a different coloured mouse at each position (see Fig.7.1). A handle (200mm long, 12mm diameter) with a red arrow extending from it was fixed to the centre of the dial. This handle could be turned through 360 degrees, so that the arrow could be positioned to point to any of the coloured mice. The fixing holding the handle provided enough friction for the handle to stay at any position on the dial.

The apparatus was placed on a table so that the centre of the dial was at about chest height. The child was positioned so he or she could easily grasp the handle with their dominant hand. They were then told that their task was to turn the handle so that the arrow would point to the different coloured mice. The child was asked to wait until the experimenter told them which mouse to turn to before moving. They were also asked to point the arrow "right on the mouse's nose". This last constraint was to increase the accuracy demands of the task. It was explained to the child that they should not let go of the handle whilst turning it to the mouse. Children were given four practice trials before the experiment was started. There were 16 experimental trials, in which the

children were asked to turn the handle each of the four target positions (1,4,5, and 8) four times. Order of presentation was randomised within blocks. The starting position of the arrow was always directly opposite the target position on the dial. The experimenter indicated the target position by the colour of the mouse at that position, and also by pointing to the target mouse.

Before presenting the results of this experiment it will be useful to show how adults typically perform this task. The data in Fig. 7.3 is taken from Rosenbaum (1993), and shows the proportion of grips that started with the thumb towards the arrow for the four target positions used in this experiment. Two points are clear from this graph. Firstly, that adults planned their movements so their hands would end up on a comfortable position at the end of the movement. When position 1 is the target, the starting position of the arrow is at position 5, and most subjects chose to grip the handle with the thumb towards the arrow in order to turn it to point to position 1 at the top of the dial. When the target is position 4 or 5, most subjects chose to grip the handle with the thumb away from the arrow. Secondly, end-state comfort planning gives rise to a characteristic V-shaped function on the graph.

7.4 RESULTS

The mean proportion of thumb-towards grips for each age group at each target position is displayed in Fig. 7.4 for normal controls, and in Fig. 7.5. for children with WS. Two points are apparent from Fig. 7.4. Firstly, in typically developing children

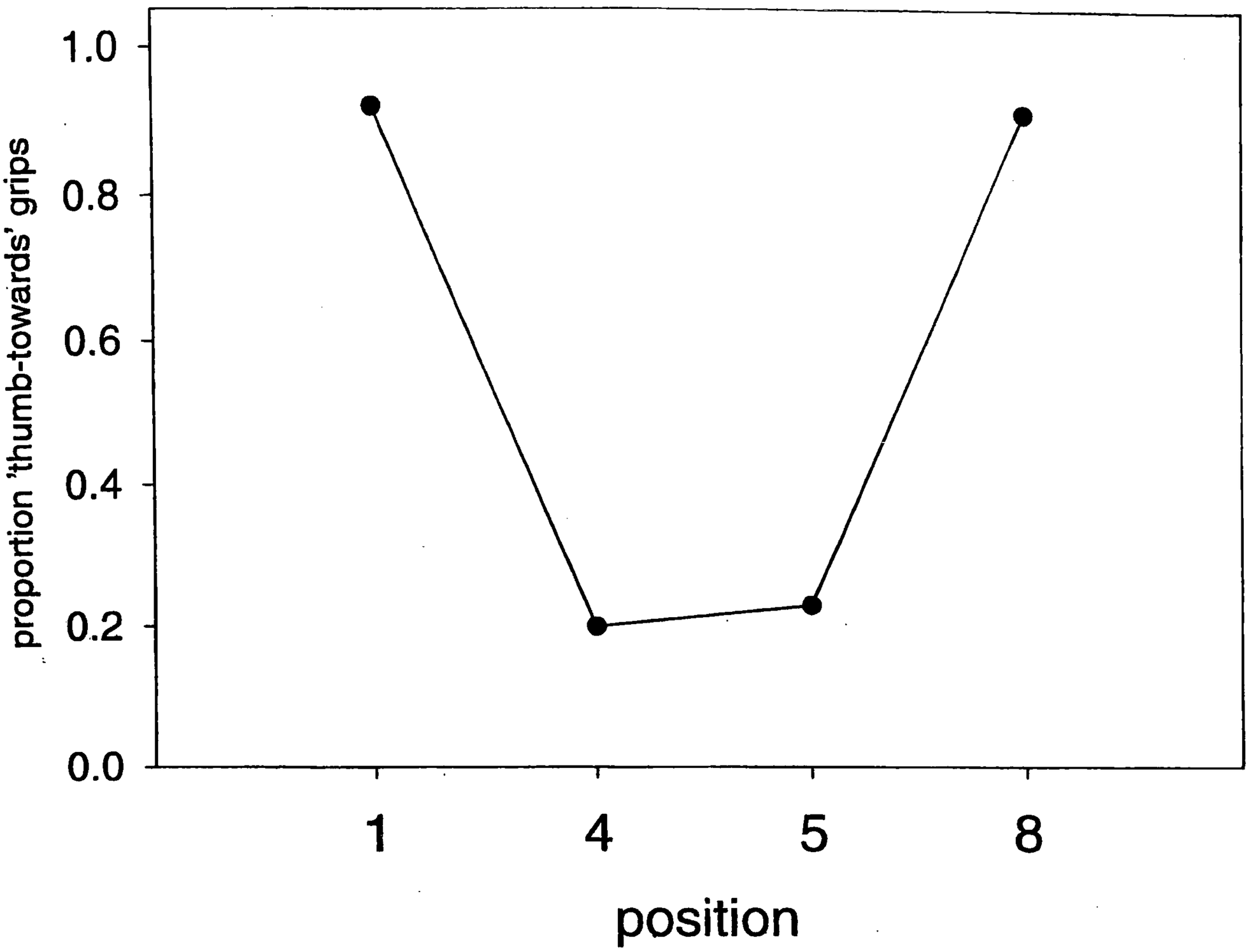


Figure 7.3 Proportion of grasps with thumb towards the handle made by adults (data from Rosenbaum et al.,1993)

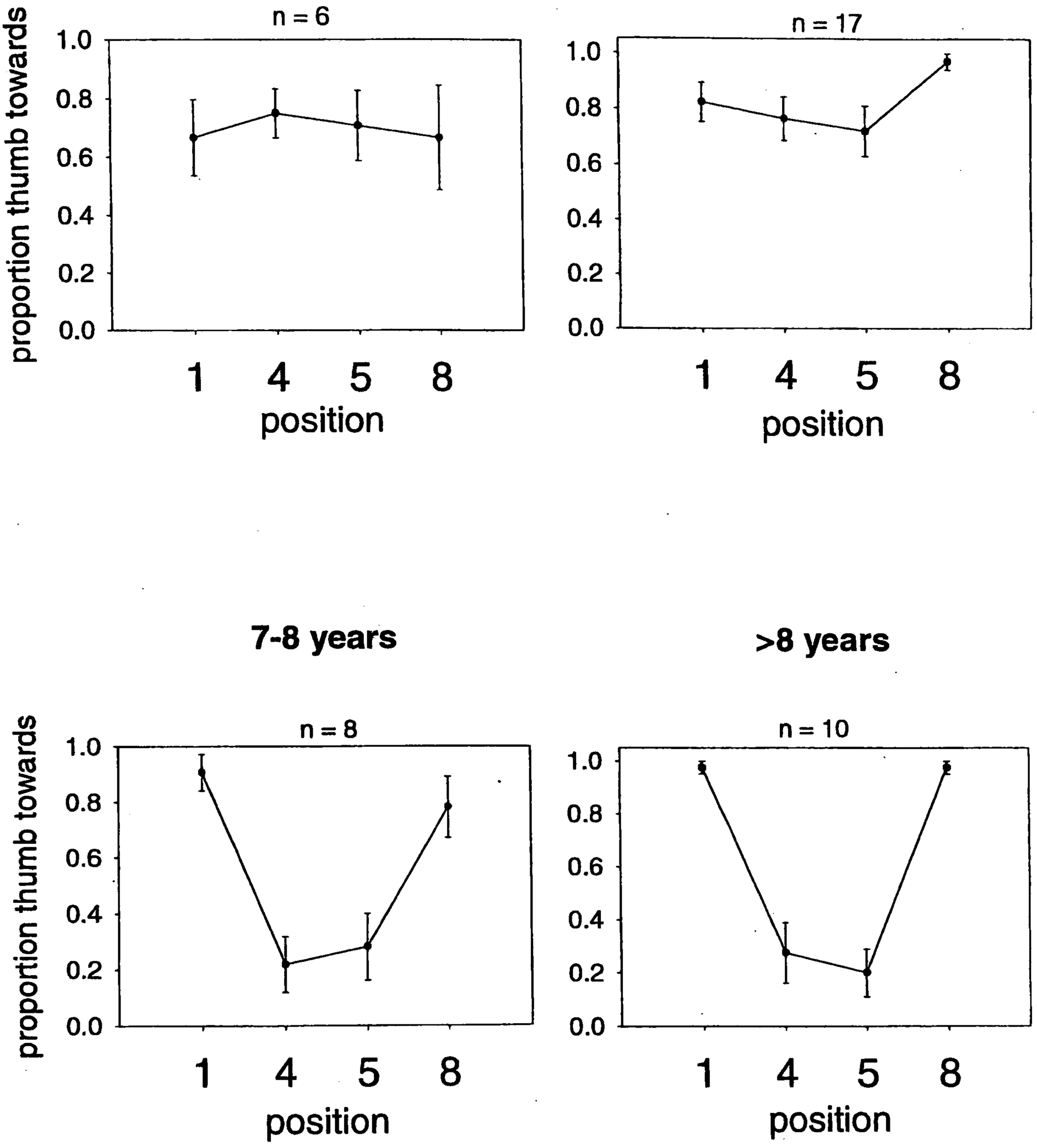


Figure 7.4 **Control children** grouped by chronological age: Proportion of thumb towards grips at each target position.

error bars are plus or minus 1 SE.

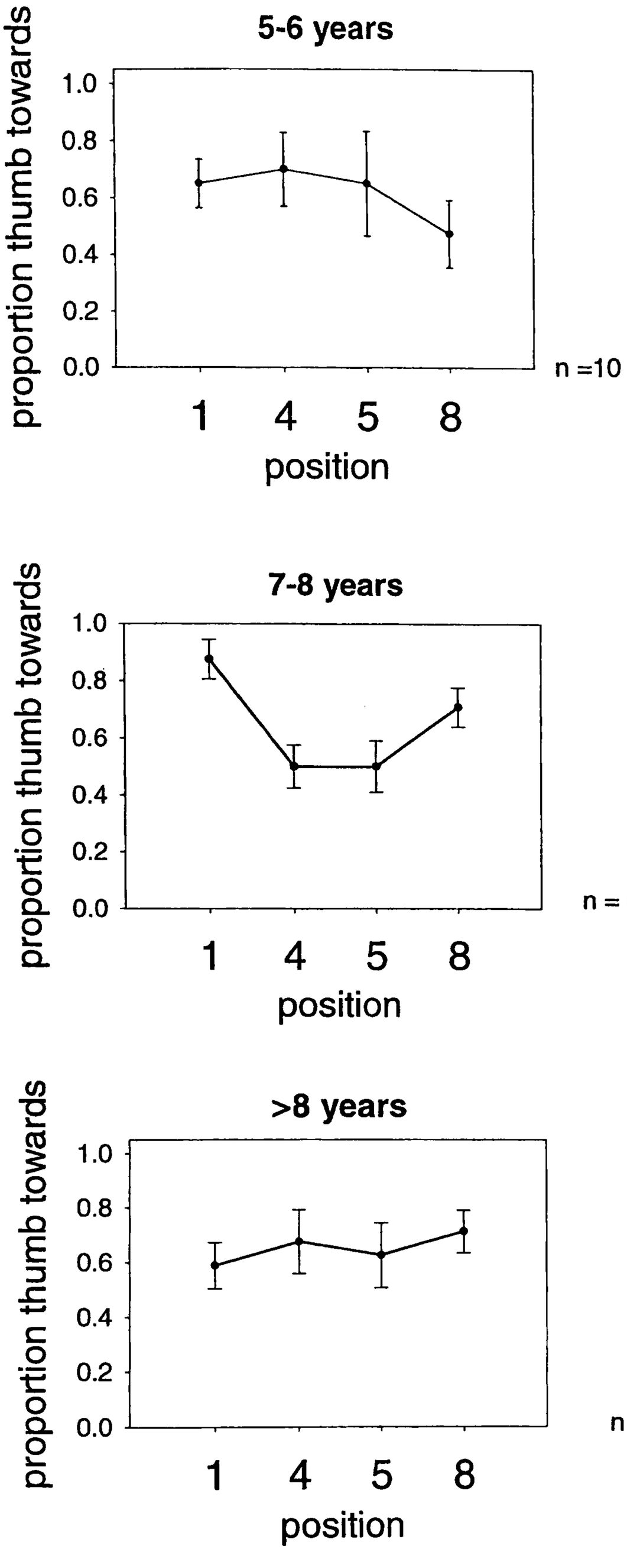


Figure 7.5 **WS children** grouped by chronological age:
Proportion of thumb towards grips at each target position.

error bars are plus or minus 1 SE.

there is a clear developmental trend in performance. The characteristic V-shaped pattern of responses to the target positions, which indicates that subjects are planning for end-state comfort, emerges at about 7-8 years of age. (This result replicates that of Smyth and Mason, 1997). Secondly, the youngest control children show a majority of thumb-towards grips at all target positions. The main developmental trend is a change from thumb towards to thumb away grips at target positions 1 and 8. However, when we look at the data from children with Williams syndrome aggregated together, the clear developmental trend is not present. There is a shallow V-shape in the 7-8 year old group, but this is not present in older children. In addition, the level of thumb towards grips is lower in the WS children, suggesting that they are using different reaching strategies from the control children.

Results were analysed separately for the two groups of children, using a 4 x 3 mixed model ANOVA, with position as a within subjects factor, and age group as a between subjects factor. For normal controls, there was a main effect of position ($F(3,96) = 6.19$, $p<0.001$) and age group ($F(2,32) = 11.86$, $p<0.001$). There was also a significant interaction between position and age group ($F(6,96) = 6.19$, $p<0.001$), indicating that the pattern of responses to the four positions differed between age groups. For children with WS, there were no significant main effects or interactions. The absence of main effects or interactions in the WS data indicates that when data from children with WS is aggregated there is no age-related trend towards choosing grips on the basis of end-state comfort.

In order to test whether performance on the handle task is related to a measure of mental age rather than chronological age, WS scores were replotted as a function of British Picture Vocabulary age equivalent. From Fig. 7.6 it can be seen that again in the grouped data there is no clear developmental trend towards end state comfort planning.

However, grouping the WS data hides a lot of variability in performance, as can be seen from Fig. 7.7 which shows the proportion of 'end state comfort' scores plotted as a function of the (chronological) age of child, for WS children and controls respectively. The mean scores for control children are shown for reference, plotted by age group against the mean age of the age group.

Regression analysis was used to test the relationship between the age of the child and the proportion of trials in which an 'end-state comfort' grip was chosen. For children with WS there was no increase with age in the proportion of end-state comfort grips, the F ratio of the overall regression was less than one, Rsq = 0.05. For normal controls the regression was significant $F(1,38) = 21.4$, $p<0.001$, and the Rsq was 0.36, indicating that the proportion of thumb-towards grips increased with age.

Individual scores were again replotted as a function of BPV age equivalent. From inspection of Fig. 7.8 it is apparent that WS children's scores on the handle task are closer to those of children of equivalent (verbal) mental age than chronological age. Indeed, a regression testing the relationship between end-state comfort score and BPV age was significant, $F(1,36) = 5.0$, $p<0.04$, Rsq = 0.35. However, there is still a subset of children with WS with a BPV age over 7 who do not show evidence of advance planning in this task. Thus, 8 WS children with a BPV age equivalent over 7 score below 50%, whereas no typically developing children over 7 years score this low.

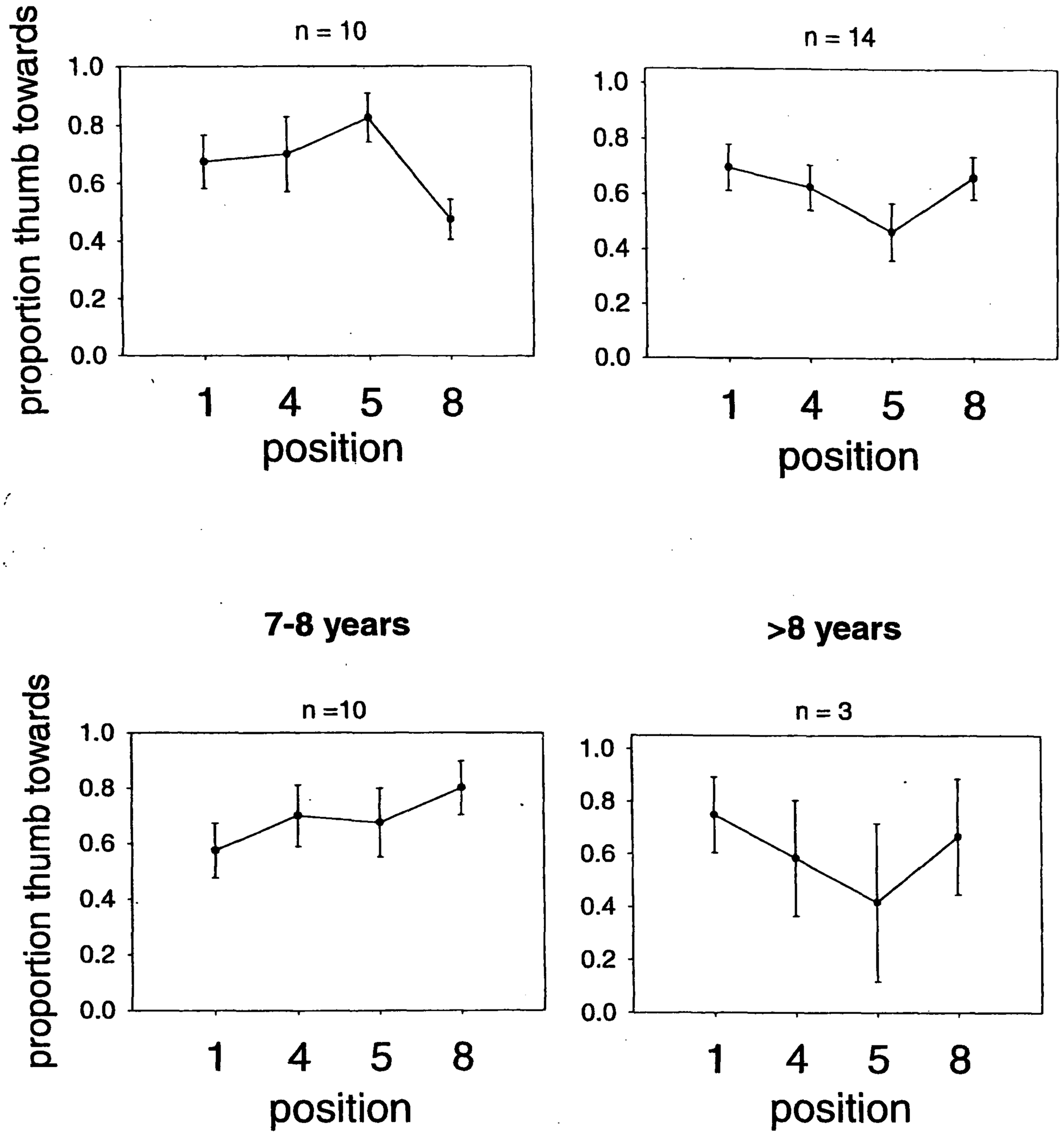


Figure 7.6 **WS children**, grouped by BPV age equivalent: Proportion of thumb towards grips to each target position

error bars are plus or minus 1 SE.

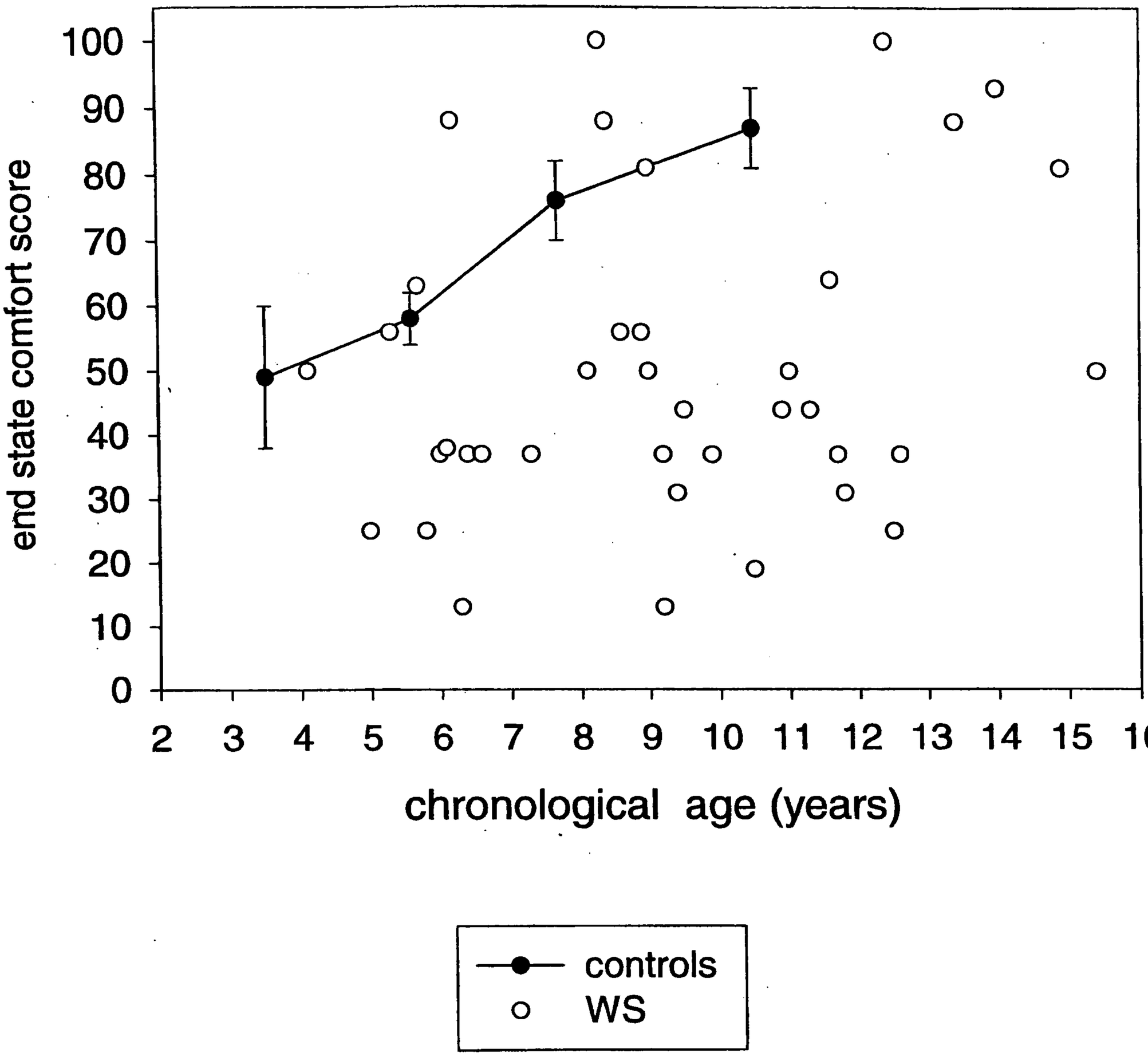


Figure 7.7 End-state comfort scores on the handle task for WS
The mean scores for control children are shown for reference, plotted by age group against the mean age of the age group.

error bars are plus or minus 1 SE

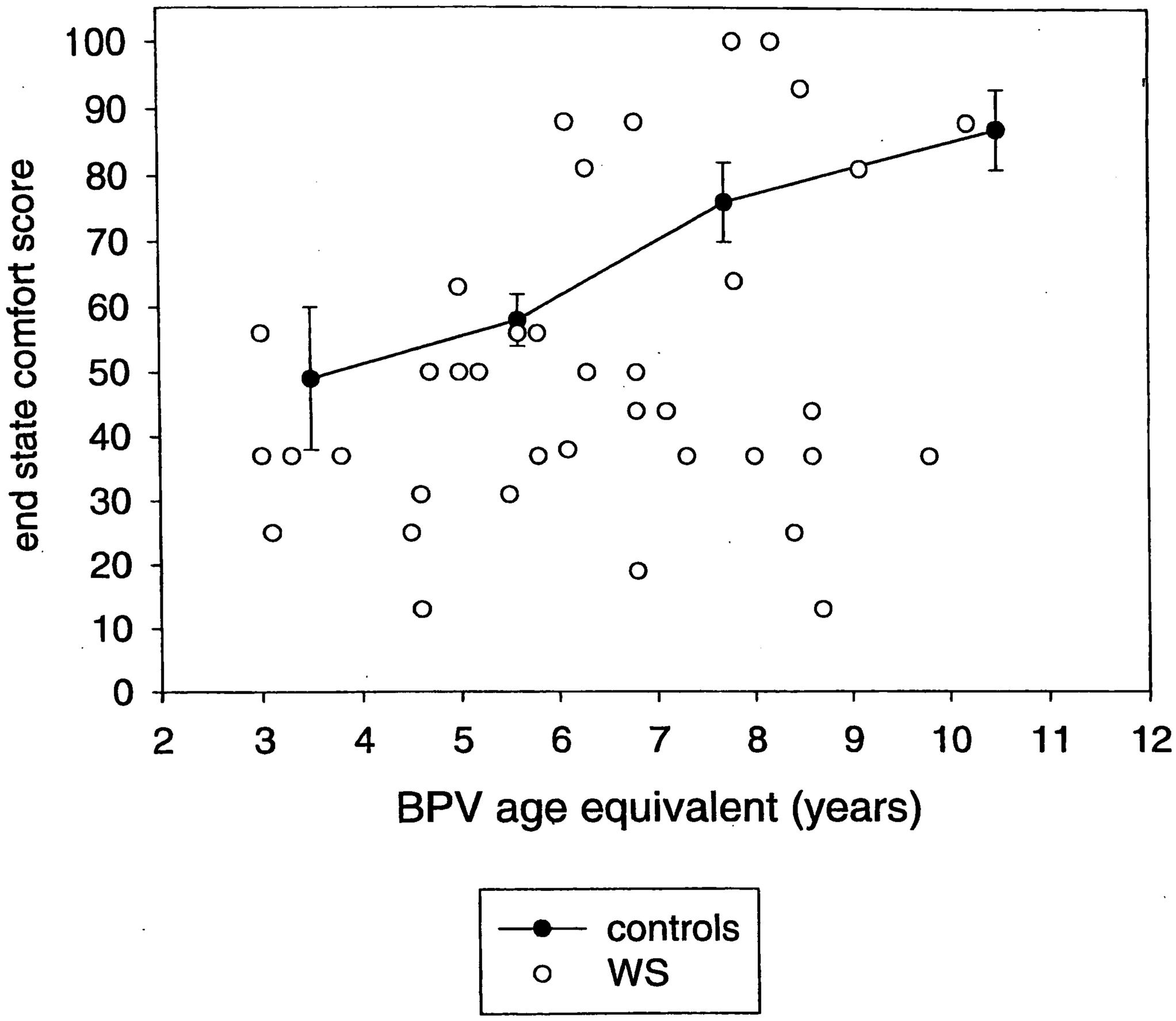


Figure 7.8 End-state comfort scores on the handle task
Scores re-plotted as a function of BPV age equivalent

error bars are plus or minus 1 SE

7.4.1. Reaching strategies

In order to clarify which reaching strategies children in this study were using, the proportion of thumb-towards grips at the top of the dial (positions 1 and 8) and the bottom of the dial (positions 4 and 5) were aggregated together. The rationale for this is that the four reaching strategies outlined above give rise to different predicted grips for targets at the top and bottom of the dial (see Fig. 7.2 and Table 1). Figures 7.9 and 7.10 show the proportion of thumb-towards grips for target positions at the top of the dial plotted against the proportion of thumb-towards grips for target positions at the bottom of the dial for control children and WS children respectively.

Table 7.1. Expected proportion of thumb-toward grips predicted by each strategy for target positions at the top (1, 8) and bottom (4, 5) of the dial.

	Strategy			
Target Positions	Stereotypical	Thumb-towards	Thumb-away	Planned
1, 8.	low	high	low	high
4, 5.	high	high	low	low

From these figures it can be seen that many typically developing children under 6 years tend to reach with the thumb towards the arrow at all target positions. It is also apparent that the main developmental trend in typically developing children is the drop in the proportion of thumb-towards grips chosen when the target is at the bottom of the dial. Children with WS, on the other hand, show a more mixed pattern of performance. Many reach stereotypically, reaching out and grabbing the handle with the thumb facing upwards regardless of target position. The thumb-towards bias at positions 1 and 8 is

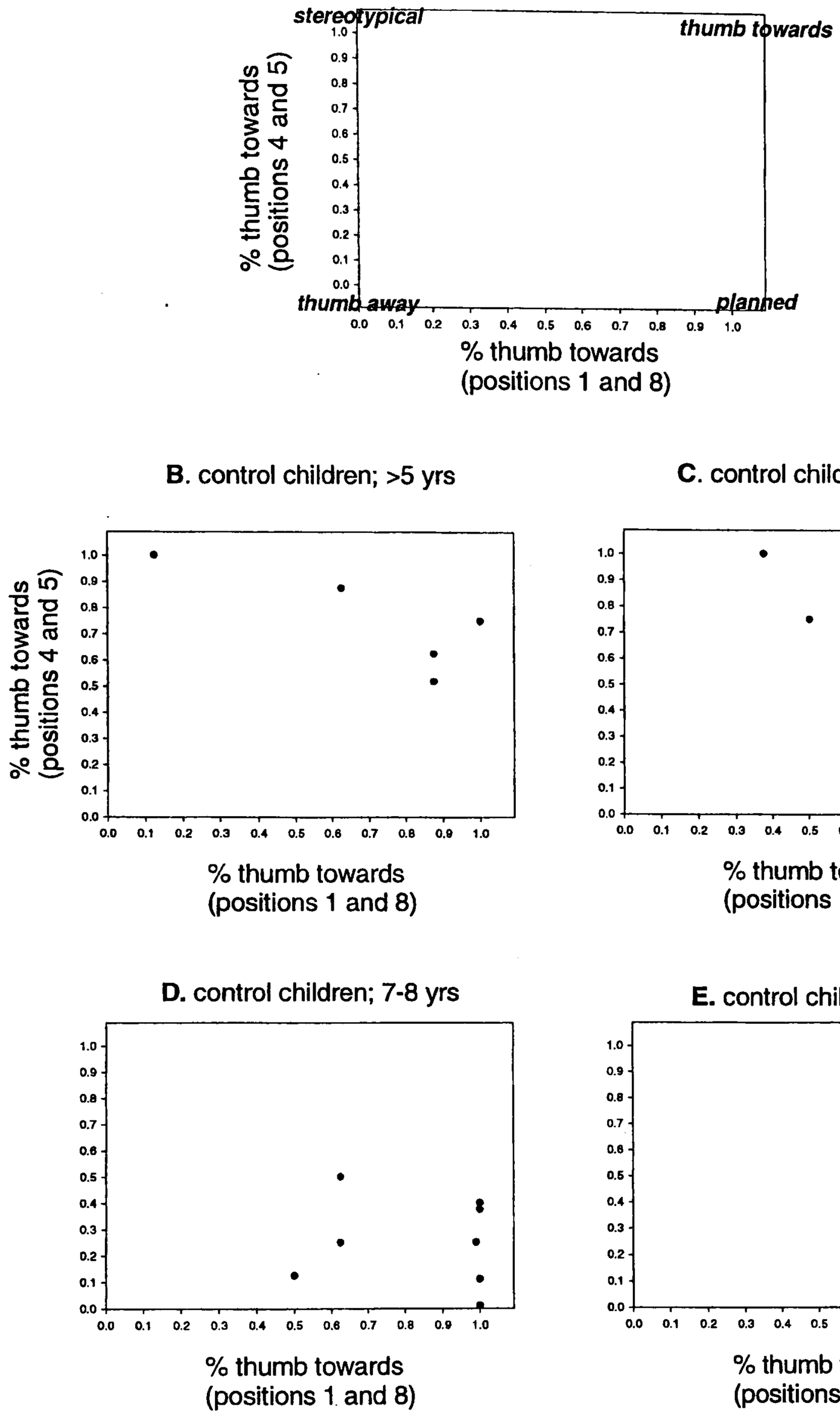
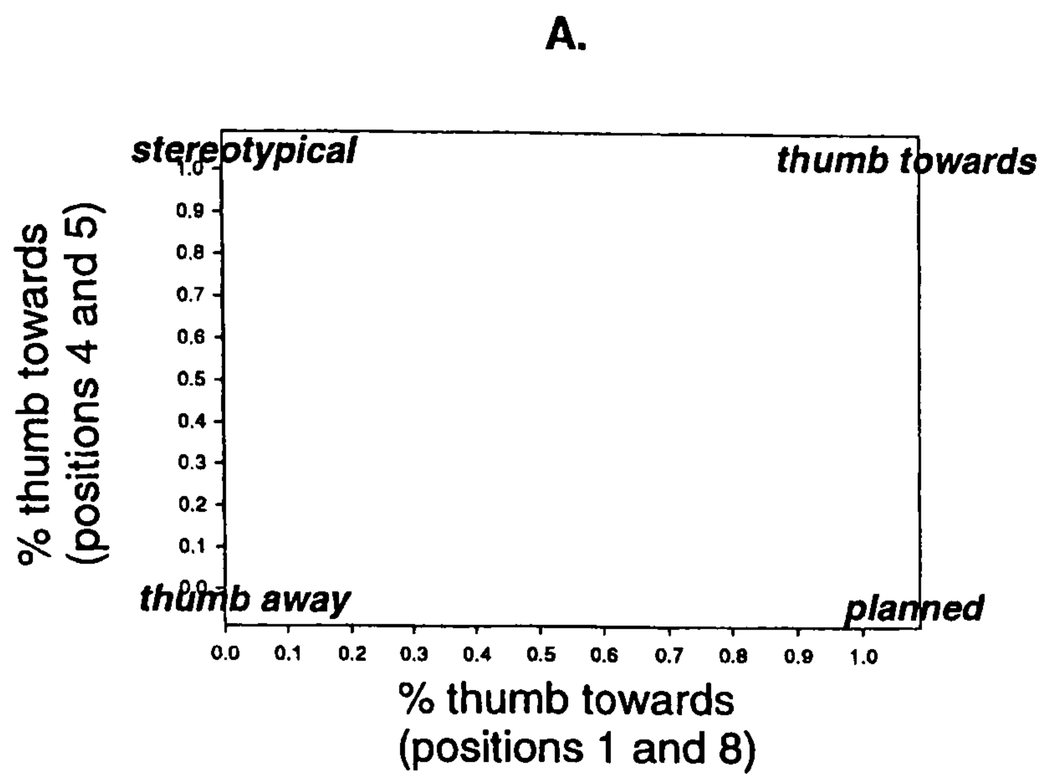
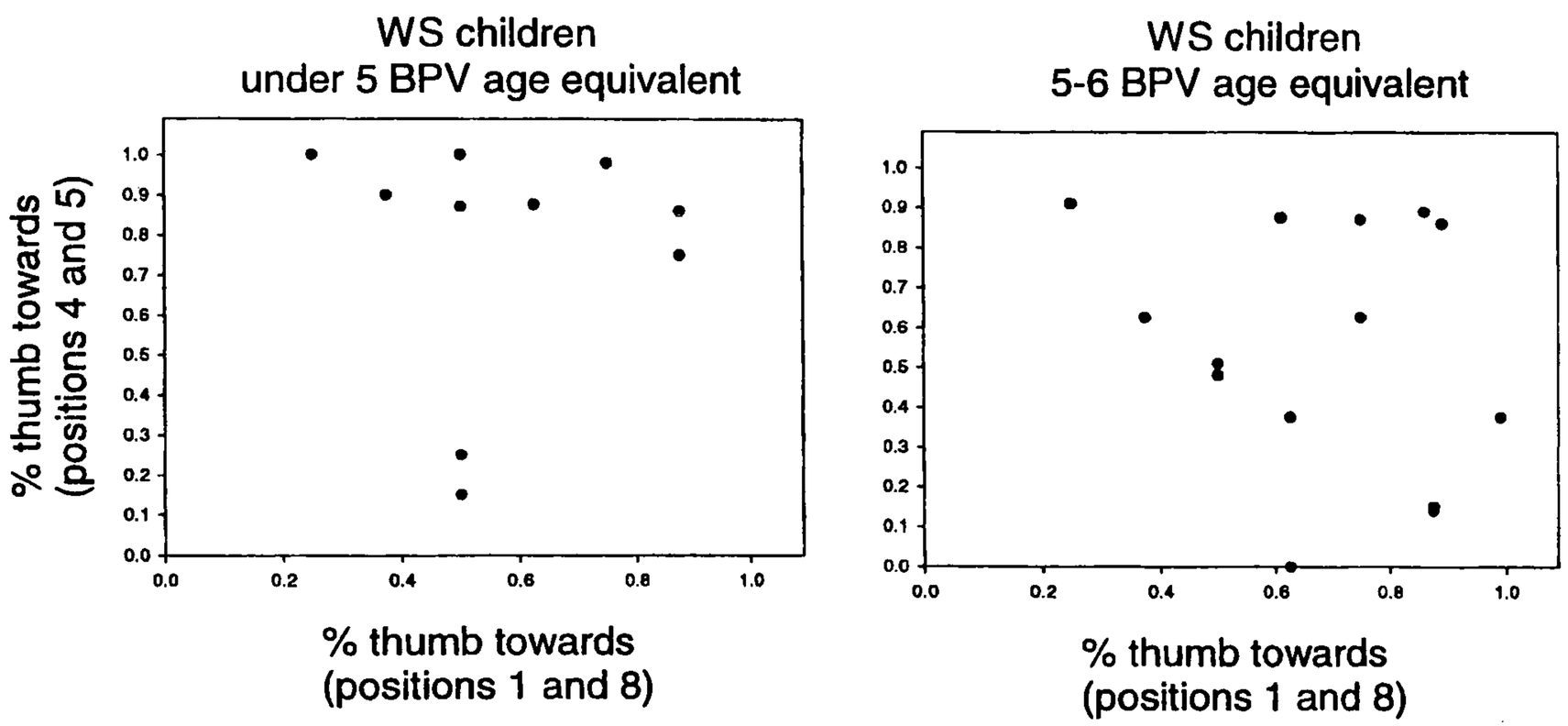


Figure 7.9 **Control children**. The proportion of thumb-towards grips for target positions at the top of the dial plotted against the proportion of thumb-towards grips for target positions at the bottom of the dial. (A) Idealised plot showing predicted positions for children using each of the four strategies. (B - E).





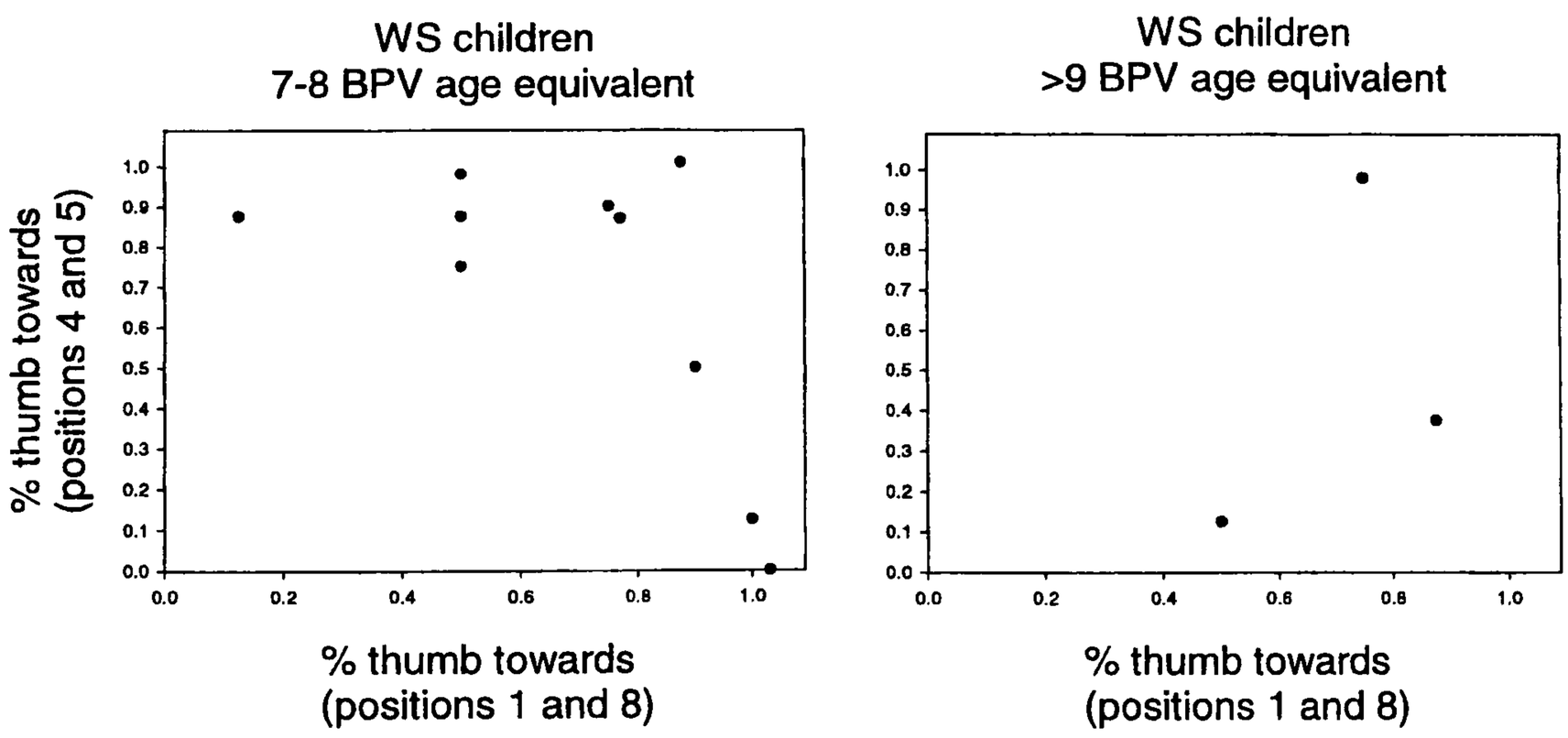


Figure 7.10 **WS children**.. The proportion of thumb-towards grips for target positions at the top of the dial plotted against the proportion of thumb-towards grips for target positions at the bottom of the dial. (A) Idealised plot showing predicted positions for children using each of the four strategies. (B - E)

less apparent. In addition, many children show inconsistent grip choices, with many, for instance, equally likely to choose a thumb towards or thumb away grip to target positions 1 and 8.

7.4.2. Correlations with tests of Frontal lobe function.

It is possible that that the difficulty that some children with WS have with this task is due to an inability to inhibit a familiar or obvious action. If this is the case, it might be expected that children who perform poorly on the handle task would also score poorly on other tasks which test the ability to inhibit a predominant response. The development of the ability to inhibit such responses has been associated in both human infants and monkeys with the maturation of dorsolateral prefrontal cortex (Diamond 1993) and patients with damage to frontal lobe find tasks that involve the inhibition of a predominant action difficult (Shallice 1988). As many of the WS children tested also carried out tests of frontal lobe function during their visit to the VDU, a comparison of scores on those tests was possible. The three tests of frontal lobe function were the Day/Night task, which requires inhibition of a familiar verbal response, a counterpointing test, which requires the child to point to the opposite side of the screen from a stimulus and a detour box task, which require inhibition of a familiar manual response. (These tests are described and results fully reported in Atkinson *et al.* 2000b). Correlations are presented in Table 7.2. None of the correlation coefficients were statistically significant.

Table 7.2. Correlations between WS children's scores on the handle task and tests of frontal function

Frontal test	r	N
Counterpointing (Difference between counterpointing and pointing latencies).	0.17	29
Detour box (No. of errors in switch component)	0.03	25
Day/Night (No. of errors in children with <2 errors on control task)	0.14	30

7.5 DISCUSSION

The results of this experiment show that many children with WS have greater difficulty planning simple goal-directed actions than typically developing children of the same age. There are a number of possible explanations for this effect.

If the ability to plan a comfortable grip is linked to cognitive rather than motor development, then it might be expected that those WS children who have the highest verbal mental age might perform best on the handle task. This interpretation is partially supported by the correlation between end-state comfort score and BPV age equivalent. However, this correlation is weaker than in control children, and there remains the question of why a significant subset of the WS children with a BPV age equivalent over 7 years score poorly on the task. Perhaps the simplest explanation is that some children with WS find it difficult to rotate their arms, due to restricted movement in the joints.. Kaplan *et al.* (1989) report that some children with WS have joint contractures which are severe enough to interfere with daily tasks. An inability to rotate the arm at the elbow or shoulder joints might make this task difficult, in that it would be more difficult to take up the 'thumb down' position at the start of the movement. However this is unlikely to explain the results of this experiment. The design of the experiment requires

that on each trial the children take up an awkward 'thumb-down' posture, either at the beginning or end of the trial. The test of planning is whether the child can trade off initial discomfort for comfort at the end of the movement. In addition, the experimental data show that the majority of children with WS (32/37) take up a thumb-down posture at the *start* of the movement in at least 6 of the 16 trials.)

If these results are not due to purely mechanical restrictions on movement, then it is likely that many of the children with WS in this study are failing to think ahead when making simple movements in which the intended purpose of the object being used is important. This might cause difficulties for them in a range of every day tasks, such as using tools or putting on clothes in the morning. A failure to predict the consequences of movement may be caused by a number of factors. Firstly, efficient movement often requires that the action that initially seems most obvious in a given situation be inhibited. Thus in the handle task, the easiest way to grip the handle is with the thumb facing upwards. The arm is near the centre of its range of rotation, and the hand does not need to be turned as it moves to the handle from its starting position at the side of the body. A failure of inhibition may lead to children choosing the easiest initial grip without stopping to consider the consequences of the action. However, in the handle task, it is also possible that a child may see the most obvious action as being to grab the handle with the thumb facing towards the arrow on every trial (i.e use the object-driven strategy or thumb-towards strategy). This may explain the weak correlations between scores on the handle task and those on the detour reaching, counterpointing or Day/Night tasks.

Rosenbaum's model gives rise to a number of possible explanations for the poor performance of some children with WS in posture planning. Firstly it is possible that impaired memory for visuospatial arrangements means that some WS children have

difficulty in associating efficient grips with target positions. Children with WS do have problems with other tasks which tap visuo-spatial working memory. For instance, children with WS have low memory span on the Corsi blocks test, where subjects have to point to a sequence of spatial locations in the correct order (Jarrold *et al.* 1999). However memory impairments cannot fully explain the deficit, because even if an efficient posture store system is not available the option still remains to compute the consequences of each action afresh on each trial. It is therefore possible that problems with visuospatial and or visuomotor transformations lead to a difficulty predicting the consequence of action. The implication of the stored posture model is that an difficulty in early childhood with visuospatial transformation may lead to a lack of fluency in movement in later life, as instances of successful movements are less likely to have been laid down in memory. It is possible that this difficulty with the automatisation of movement may be related to cerebellar abnormalities observed in WS (for a discussion of the role of cerebellum in motor learning and the automatisation of movement, see Stein and Glickstein (1992) . Another possibility is that children with WS have a greater tolerance for discomfort than control children. This would mean that when evaluating possible end-states for predicted discomfort, similar weights would be assigned to the thumb up and thumb down position of the hand. The results of this study (and that of Smyth and Mason, 1996) also have implications for normal development of movement planning. It is apparent that before children are planning consistently for end-state comfort, they are not reaching haphazardly. To attain end-state comfort in this experiment required that a thumb-down posture be adopted, regardless of the target position. However, children tended to adopt this posture when the target position was at the top of the dial at an earlier age than when the target was at the bottom of the dial. The thumb-towards bias is therefore developmentally prior to end-state planning. This suggests that there may be a developmental transition from object based to end-state planning, from taking into

account the immediate properties of the handle to planning for the end-state of the hand. The relatively late onset of this transition may reflect the slow maturation of mechanisms in pre-frontal cortex responsible for inhibiting prepotent action and coordinating the elements of a complex activity.

The results of this experiment suggest that in the course of normal development, children move from planning reaches using only the immediate properties of the object to be used, to a planning reaches which take into account the future position of the object and the limb. Even the youngest children in this study showed the thumb-towards bias, and most typically developing children plan ahead for end-state comfort by 7 years.

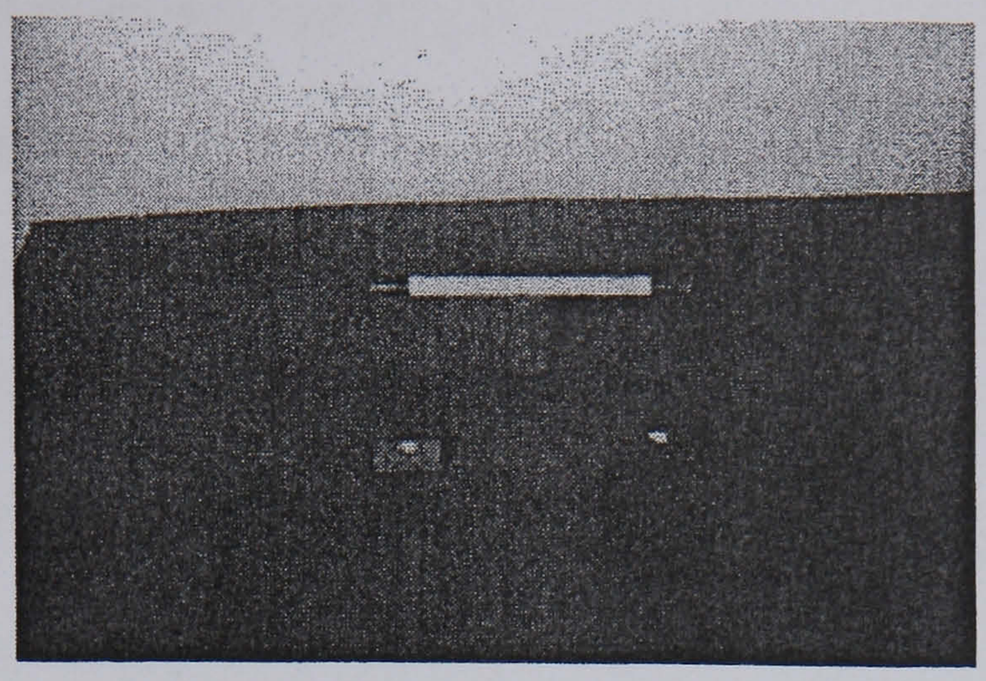
In children with WS, on the other hand, one cannot identify a typical pattern of performance. Some children with WS plan ahead at least as well as typically developing children of the same age. Furthermore, these children are spread across the age range of the study. Children with WS are also more likely to use a stereotypical 'just reach and see what happens' reaching strategy. This indicates that they are either starting the reach before they have worked out how they are going to achieve their aim, or that they are unable to visualise the required movement before acting, and are therefore forced to cope with the consequences of inappropriate grip choices. Lastly, children with WS were more inconsistent in their choice of grips during the course of the experiment, suggesting that they have trouble remembering the consequences of previous actions.

7.6 THE BAR TASK

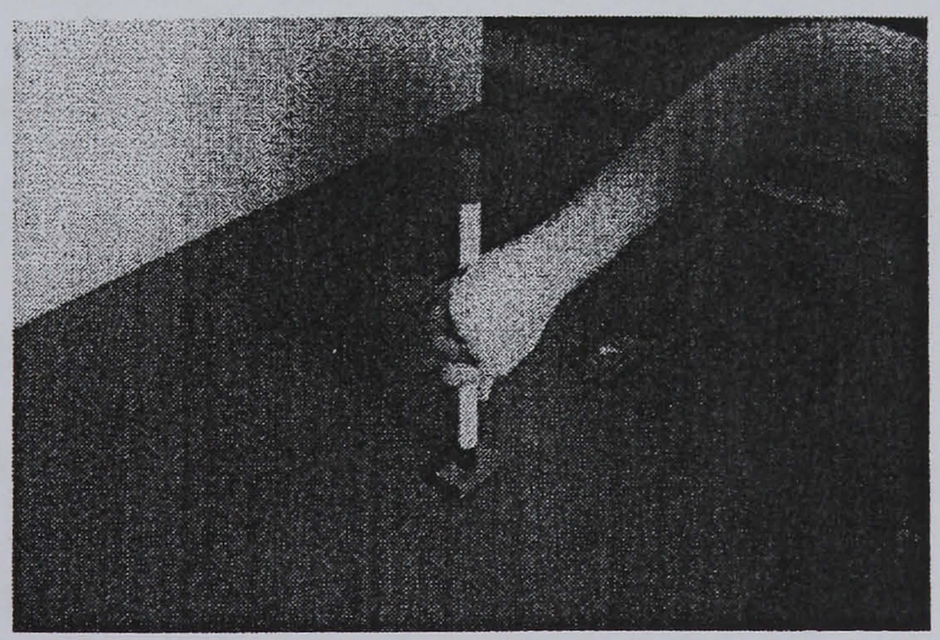
In the Bar Task, children are asked to pick up a wooden bar, and to put the end of it into a coloured hole. From Fig. 7.11 it can be seen that if a right handed person picks up the bar and puts the right-hand end into either hole, the most comfortable hand position as the bar is placed in the hole will be with the thumb facing upwards (a). This end position requires that the bar be grasped with an underhand grip as it is picked up. If an overhand grip is chosen, the hand will be in a more awkward thumb-down position as the bar is placed in the hole (b). Conversely, if the left-hand end of the bar is to be placed in the hole, an overhand grip will lead to a thumb-up hand position as the bar is inserted. The choice of grip (underhand or overhand) can therefore be used as an index of motor planning.

Whilst adults have been reported to reliably choose underhand grips on this task, previous evidence from typically developing children is contradictory. Hughes (1996) found that few 3 year olds chose an underhand grasp in this task, whereas the majority of normal children over 4 years chose an underhand grip on at least 3 out of 4 trials where this was appropriate. Hughes compared these children's scores with those of autistic children and found that a group of autistic children (with a mean VMA of 9.7 years) were significantly impaired relative to 4 year old controls.

Smyth and Mason (1997), on the other hand report that there was no improvement in the proportion of end-state comfort grasps in normal children or children with DCD between the ages of 4 and 8. However, Smyth and Mason did not test any 3 year old children, so it is possible that any dramatic improvements in performance in this task take place between the age of 3 and 4 years. Smyth and Mason also speculated that the reason for the discrepant results was a slight difference in design



(a.)



(b.)

Figure 7.11. Apparatus for the Bar task

between the two studies, resulting in a lower accuracy requirement in their task than that used by Hughes. As previous evidence suggested that end-state planning in the handle task does not develop until around 6-7 years, this experiment was designed to test children with WS on what at first sight seemed to be a simpler motor planning task, in order to investigate differences in motor planning ability between younger WS children and typically developing controls.

7.7 METHOD

7.7.1. Participants

Participants were 21 children with Williams syndrome, between 4 and 15 years and 68 typically developing children between 4 and 11 years. 22 of these children were recruited as part of a third year project carried out by a student at UCL. 14 of the children with WS also carried out the handle rotation task.

7.7.2. Apparatus and procedure

The apparatus for the bar task is shown in Fig. 7.11. It consisted of: a wooden bar 300mm long and 13mm diameter, with one end painted red and one end painted blue; two 50mm x 20mm rectangular blocks, one red and one blue; and a cylinder, 45mm diameter and 75mm high, with a groove in the top. The two rectangular blocks, each had a hole 15 mm diameter drilled in them, into which the wooden bar could be inserted. The rectangular blocks were fixed near to edge of the table, with the blue block on the left hand side. The cylinder was placed on the centre line between the blocks, but 150mm behind them. At the start of each trial, the wooden bar was placed in the groove on the top of the cylinder, with the blue end of the bar to the left of the subject.

Before each child started the experiment, the experimenter checked that they knew the colours red and blue. Each child was given practice in the task, by placing the bar upright in the holes a number of times. The hole was only just big enough for the bar to fit into it, so an accurate placing movement was required on each trial. The experimenter then asked each child to place each coloured end into each hole four times, in a preset randomised order, giving 16 trials overall. The dominant hand was used for all trials.

7.8 RESULTS

Only those trials where an underhand grip would lead to a comfortable thumb down position were scored. For a right-handed child, these were the eight trials in which the right-hand end of the bar had to be placed in the holes. The rationale for this procedure is that the overhand grip is the dominant grip for this task (Rosenbaum *et al.* 1990) and therefore clear evidence of planning can only be shown when children make an unusual response to solve a problem (Hughes, 1996). The number of trials (expressed as a percentage) in which children chose an underhand grasp is plotted as a function of age in Fig. 7.12. Two points are notable, firstly, there is considerable variation in the proportion of underhand grips used by children in both groups at any given age. Secondly, this data suggests that reliable choice of underhand grips seems to be a characteristic of older adolescent and adult subjects. When the data from WS children are replotted as a function of BPV age equivalent, the difference between the groups is even less apparent. Interestingly, when these relationships were tested statistically using regression analysis it was found that age was a significant predictor of scores on the bar task in control children $F(1,63) = 6.92$, $p<0.01$. However, when only typically

developing children in the same age range as the BPV age equivalents of the children with WS were included, the regression was no longer significant at the 0.05 level, $F(1,56) = 3.2$, $p<0.07$. In children with WS neither chronological age ($F(1,18) = 0.4$, $p<0.52$) or BPV age equivalent ($F(1,18)=1.24$, $p<0.28$), predicted scores on the bar test.

To determine whether there were group differences in scores between WS children and control children of equivalent verbal mental age, scores were plotted by age group (see Fig. 7.13). Two way ANOVAs, with age group and group as factors show no significant main effects or interactions, whether age groups are based upon the chronological age or BPV age of the WS children. (Age groups which contained only children from one group were excluded from the analysis).

7.8.1. Correlations with tests of frontal lobe function

Correlations between scores on the bar task and scores on the three tests of frontal function are displayed in Table 3. None of the correlations were statistically significant.

Lastly, the correlation between scores on the handle task and the bar task was calculated, to test whether they measure the same ability. Handle and bar scores are significantly correlated in the control children who performed both tasks, $r(36) = 0.5$ $p<0.002$ but not as strongly in WS children $r(14) = 0.49$ $p<0.07$.

Table 7.3. Correlations between WS children's scores on the bar task and tests of frontal function

Frontal test	**r**	**Sig. (2-tailed)**	N
Counterpointing (Difference between counterpointing and pointing latencies).	-0.45	0.10	14
Detour box (No. of errors in switch component)	0.39	0.23	11
Day/Night (No. of errors in children with <2 errors on control task)	-0.19	0.52	14

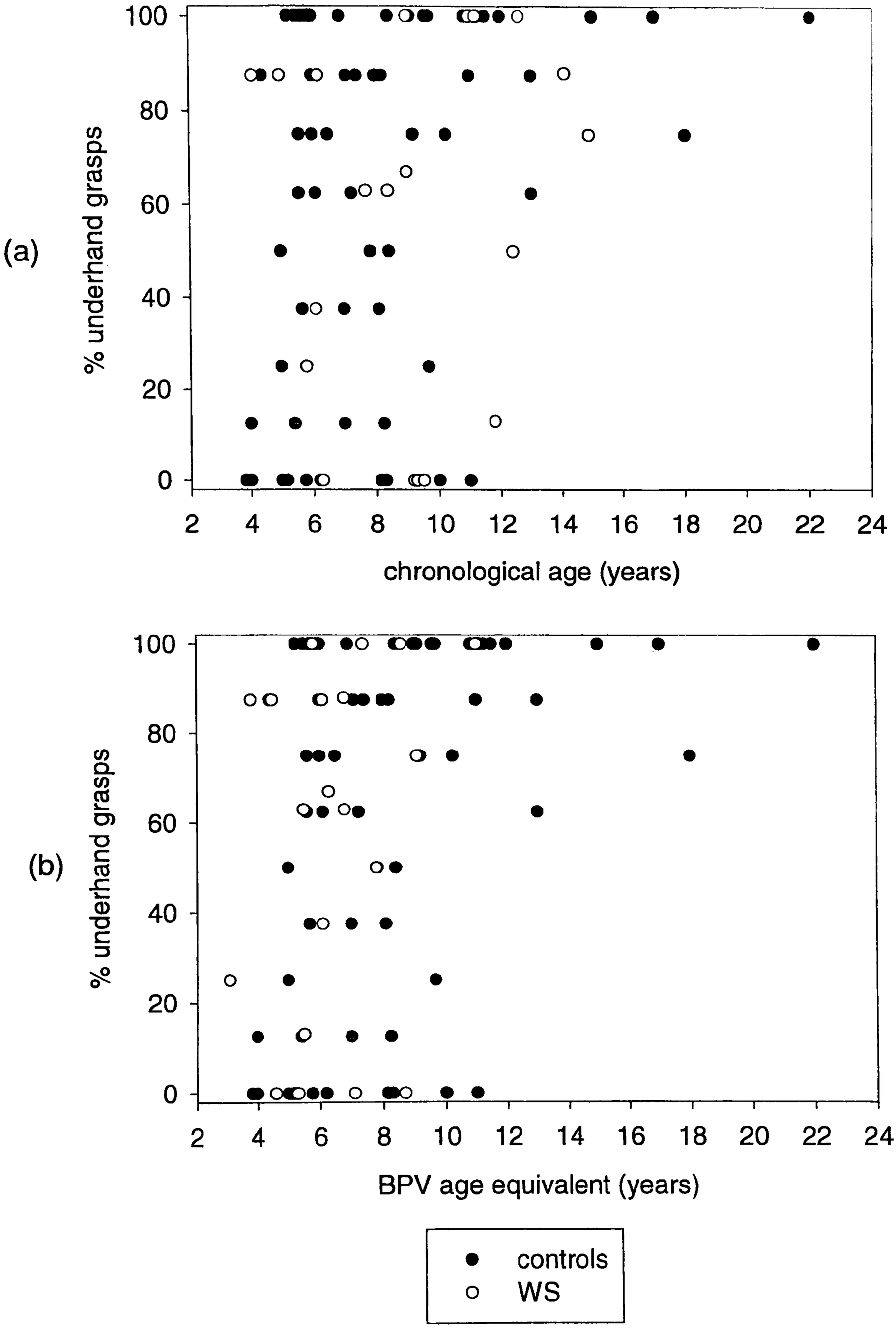


Figure 7.12 Scores on the bar task plotted as a function of (a) chronological age, and (b) with WS scores re-plotted as a function of BPV age equivalent

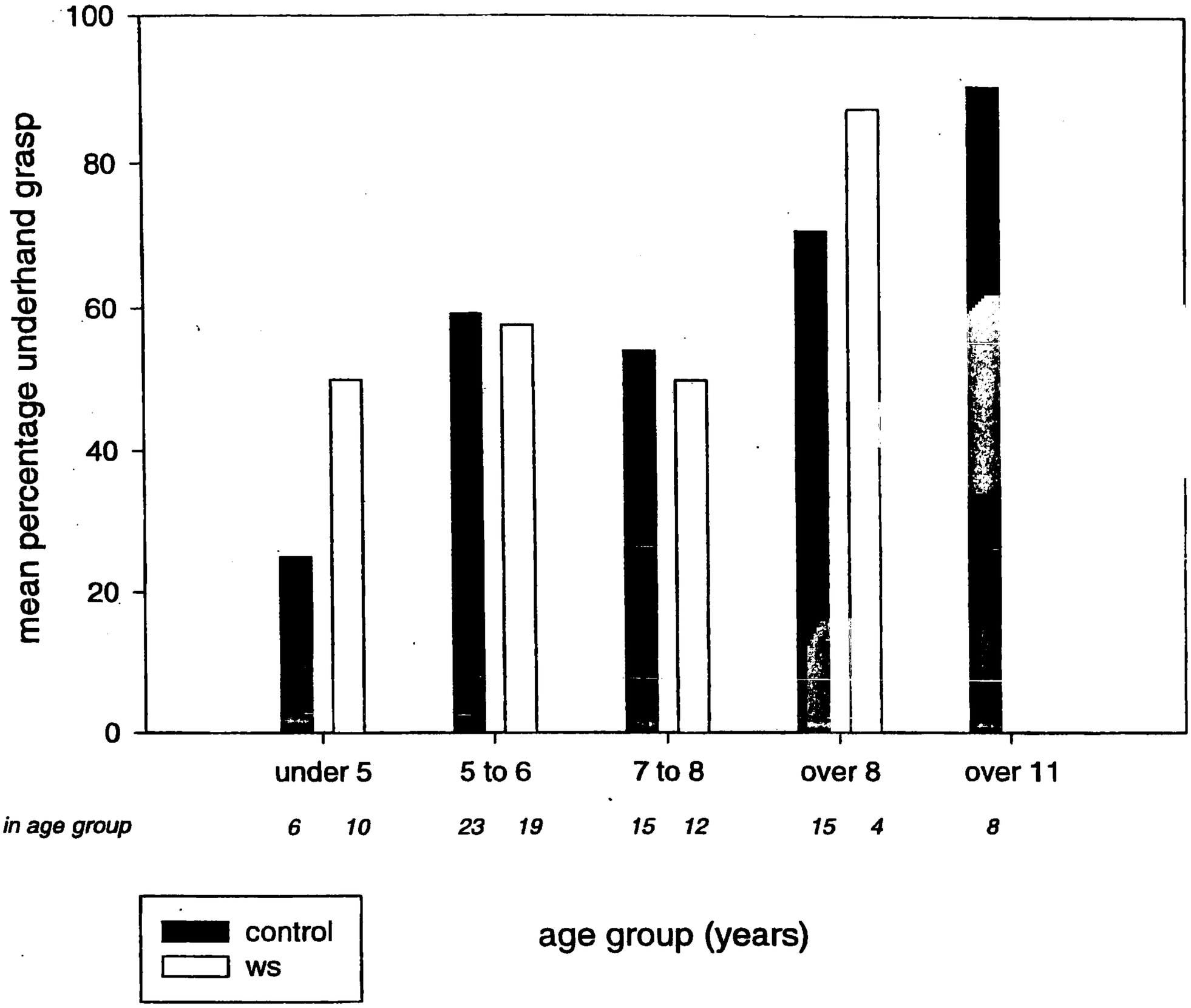


Figure 7.13 Mean scores on the bar task, compared by age group.

7.9 DISCUSSION

WS children and controls of equivalent verbal mental age do not differ in their ability to perform the bar task. This seems to be due to the considerable variation in control children's scores at least up to 10 years. Contrary to the finding of Hughes (1996) there does not seem to be a clear cut-off age after which children consistently choose underhand grips in this task. The version of the task used in this experiment required the child to put the bar into a hole, as in Hughes' task, and unlike in the task used by Smyth and Mason. The difference between Hughes' results and those of this study and Smyth and Mason's are therefore unlikely to be a result of different accuracy requirements in the tasks. As Short and Cauraugh (1999) found that increasing the accuracy requirements in a similar task increased the frequency of end-state comfort grips, it would be useful to test for the same effect with children, by reducing the diameter of the bar and hole. Why does this task, which seems at first glance to be simpler than the handle task, not show such a clear-cut developmental trend in end-state planning? Perhaps the simplest explanation is that whilst success on both tasks involved avoiding a relatively uncomfortable thumb-down position of the hand, in the case of the handle task the arm is extended when positioning the arrow, whereas in the bar task, the arm is bent, and the hand closer to the body. If the reader tries putting the hand in a thumb-down position, pointing towards the desk, it should be apparent that that the tension in the arm muscles is greater when the hand is extended than when it is close to the body. It may be the case, therefore that there is less incentive to avoid the thumb down position in the bar task than the handle task.

8 Conclusion

8.1 TYPICALLY DEVELOPING INFANTS

In Experiment 1 infants were presented with objects that differed in size only. This was to compare the preferences of systems selecting a target for a reach with those controlling visual orientating responses. It was predicted that the systems controlling reaching would become progressively more attuned to visual inputs which signal the graspability of an object. Thus, if infants avoid reaching for unwieldy objects, this implies either that ventral stream mechanisms are attuned to visual inputs which signal the graspability of an object, and can communicate this information to the dorsal stream, or that implicit object processing in the dorsal stream can influence target selection (Rizzolati, 2000). A successful execution of the reach implies that parameter specification mechanisms in the reach and grasp channels of the dorsal stream are operative. It was an open question whether the systems controlling looking would be activated by grasp-related object attributes, or by a more general visual salience. However, if the first look is directed mostly to the smaller object, this would imply that grasp affordances can activate target selection mechanisms for visual orienting as well as reaching.

There was no evidence from Experiment 1 that visual orienting mechanisms are sensitive to grasp affordances in infancy. First looks did not tend to be towards smaller objects, and there were no differences in the duration, or frequency of looking to any of the objects. Rather, there was a consistent tendency in all experiments for infants to look first at the largest object presented to them. This may be because the direction of first look is influenced by a system which is orienting to the largest patch of contrast in

the visual field. On the reaching side, this experiment did show that systems controlling prehension become gradually more tuned to grasp affordances. In addition, there was some evidence that looking and reaching may be 'yoked' in early infancy. The youngest infants in this study tended to reach during the first fixation, towards the object being fixated, whereas those infants who reached most for graspable objects looked back and forth between the objects more frequently. This early look-reach response may allow infants to correlate visual and tactile experience of objects in the world around them.. It would also allow them to gain experience of getting the arm to a visually defined target. A later development is the ability to inhibit this early exploratory impulse. This allow infants time to make a selection between objects which is based upon visual information alone.

In experiment 3 an attempt was made to manipulate this link between looking and reaching by testing whether looking preference would influence reaching preference. It was reasoned that if looking and reaching systems are 'free' to select independent targets, then an increase in visual salience should only increase the likelihood of a look to an object which is too large to grasp. But if selection for action mechanisms are not fully differentiated during first year, this might also increase the likelihood of a reach.

The data from experiment 2 showed that looking and reaching responses are not fully independent in the first year of life. Preferential looking measures showed that infants looked first most often at the face object, and preferential reaching measures showed that a corresponding decrease in the number of reaches to the graspable object when it was paired with the face object. In this experiment, then, infants seemed use their 'knowledge' about grasp affordances less reliably in trials where the competing object was more visually attractive.

The combination of looking and reaching measures taken, on the same subjects, during the reaching task made it possible to show both age-related and context-specific changes in selection for action in infants. Firstly, in experiment 1, a transition was noted from a tendency to reach to the first object fixated in any given trial, to an increasing ability to select an object according to its potential for manipulation. Measures of the number and duration of fixations confirmed that this transition was accompanied by an increase in looking back and forth between the objects before reaching. Thus the tendency to reach for the first object looked at might be caused by a difficulty in inhibiting an impulsive general orientation mechanism which includes both eye and arm movements, or alternatively a difficulty in disengaging visual attention from the first object looked at.

The fact that both looking and reaching preferences were recorded also made it possible, in experiment 2, to demonstrate that looking and reaching preferences were influencing each other on a trial-by-trial basis. Reaches where the target of the first look and the reach were the same were more likely to be made to the face object. In addition, late corrections to the reach were more likely to be towards the graspable object. This experiment confirms that infants tend to reach where they look. However, as looks are drawn to the most visually salient object, this tendency sometimes conflicts with a developing target selection process which takes into account the grasp affordances of objects.

The kinematic measures of infant reaching showed that when infants start to appreciate that smaller objects are easier to grasp, the kinematics of the reach change. In experiment 1, reaches made by infants between 8½ - 12 months, who showed a preference for reaching for smaller objects, were slower overall, and showed a longer deceleration phase than reaches made by younger infants. These results can be related

to other work which has shown that infants' reaches show higher velocity and shorter duration when visual information about the target is reduced (Clifton *et al.* 1994). The likelihood is that the youngest infants are making less use of visual information about the target, and this results in faster, more ballistic movements. In addition, when adults reach to small or difficult to manipulate targets (Weir, 1994), the length of the deceleration phase increases.

In experiment 3, there were similar age related changes in reach kinematics. In addition, reaches where the target of the first look and the first reach were the same took less time, had a shorter 'homing in' period and were more ballistic (had fewer peaks in the hand speed profile). Again, it is likely that these more impulsive reaches were making less use of visual information about the target.

A question that has informed this thesis throughout is whether one can identify the operation of different visuomotor subsystems contributing to motor output in the course of development. Because of the probability of complex interactions between the various systems controlling looking and reaching, it is of course difficult to make inferences about the neural systems that influence infants' behaviour when they are presented with a choice of objects to reach for. However, as stated in chapter 4, the evidence presented here shows that the ability to visually scan a scene and select a suitable target for action depends not only upon developing target selection processes (the inhibition of all but one of the potential actions elicited by a visual scene), but also on inhibition between systems controlling looking and reaching. These experiments support the view that the ability to inhibit a reach to the object being fixated is one that develops in the early stages of reaching. However, an initial linkage of looking and reaching may be functional in that it provides an impetus for infants to gain experience of objects and to increase accuracy and control in visually guided reaching.

8.2 CHILDREN WITH WILLIAMS SYNDROME

Working with the research group in the Visual Development Unit made possible a study of the development of the visual guidance of action in children with Williams syndrome, a population in which it has been suggested that the dorsal stream of visual processing may be selectively impaired (Atkinson et al. 1997, Reiss et al. 2000).

The aim of the first study involving children with Williams Syndrome was to test the hypothesis that spatial and visuomotor deficits seen in WS are symptomatic of a deficit in the dorsal stream of visual processing relative to the ventral stream. Kinematic measures showed that children with WS do show subtle differences in performance from control children when reaching to objects of different sizes. Some children with Williams syndrome showed a poor adaptation of the grasp to the size of the object. In addition, there was evidence that WS children were making smaller adaptations of grip size to changes in object size than were control children. However, it was clear that WS children also performed consistently worse than controls on the perceptual matching element of the task.

There was no evidence, then, of a simple dissociation between perceptual and visuomotor responses to object size. How does this leave the proposal that WS cognitive profile involves a relative preservation of object recognition and comparison skills, which are thought to depend upon the ventral stream of visual processing? It is clear that there is further work to do in specifying exactly which abilities are preserved in WS. There are clear strengths shown in the Benton face recognition test, in which one face must be chosen which matches one of six target faces (Wang *et al.*, 1995, Pezzini *et al.* 1999). However, WS children find it much harder to match a choice

square with one of a range of squares of different sizes. Both tasks involve matching a choice stimulus to one of a range of target stimuli. What distinguishes these two tasks? It is possible that face processing is a special case of ventral-stream processing that is preserved in WS (Atkinson, 2000). However, children with Williams syndrome perform well on recognition tests using objects other than faces, such as in the non-canonical views test (Wang, 1995), or in the shape matching element of the ABCDEFV (see section 6.3.5). When matching faces, or even simple geometrical shapes, a range of strategies are available. One can one can base the discrimination on the size, or shape, of individual features, or on the interrelationships amongst the component features. In the size matching task, however, the discrimination must be based upon the magnitude of a single feature – the size of the square. It is possible that WS children find it difficult to appreciate metrical relationships – there is an analogy with the Benton line test, where again,, perceptually similar stimuli must be matched with a range of target stimuli which vary on a metrical scale – in this case angle of orientation.

This study also enabled a comparison of the development of reach kinematics, between WS and typically developing children. WS children moved more slowly, spent longer in deceleration and showed more movement units (number of peaks in the hand speed profile) than controls. In the discussion of the infant studies in this thesis it was proposed that a similar kinematic profile was associated with a period in development where infants in the early stages of reaching are first taking into account the visual properties of objects when planning a reach. The fact that much older children with WS show some of the same characteristics indicates that the transition to the stereotypical adult pattern of reaching may be significantly delayed in WS. Indeed, when differences in kinematic measures between children of different ages were looked at, there was evidence for an atypical developmental profile in WS. For instance, only the oldest

children showed the typical, single-peaked velocity profiles which were seen in comparison children as young as 4 years in this study, and by 2½ years in other work (Konczac *et al.* (1997).

This data also made possible a normative study of action control in typically developing children between 4 and 14 years olds. This is, to my knowledge, the first time such a study has been carried out, and so this data fills a gap in the kinematics literature. The main finding here is that whilst the kinematics of the reach in young children are broadly similar too those of adults, one measure (deceleration time, which indexes the time available make final adjustments based upon visual feedback) is gradually reduced throughout childhood. Pryde *et al.* have already shown that deceleration time is longer in 9 year olds than in adults. This study replicates and extends this finding by demonstrating that the developing motor system progressively reduces the time available for visual corrections when reaching. This indicates that the fluent, automatic pattern of performance seen in adults is the result of a long process of refinement. This may be because during childhood the motor commands for a reach must be continually re-calibrated due to the changing length and mass of the arm, and having a larger proportion of the reach under visually guided control allows a greater margin for error, until growth is completed. Alternatively, it may reflect less efficient processing during childhood, as suggested by the work of Roy *et al.* 1993, who showed that elderly people also spent more time in deceleration when reaching.

The second set of studies on WS children moved from the adaptation of action to the immediate properties of the target object (object-based planning) to the capacity adapt an action according to the motor context (end-state planning). One of the measures used (the handle task) showed clear differences between WS children and controls. Here it will be useful to look first at the typical course of development. In the

normal case there was a developmental transition from object-based to end-state planning. When performing the handle task, the youngest control showed a bias to grasping the handle with the thumb towards the arrow. This indicates a concern with the immediate properties of the object, linking the part of the hand that is associated with pointing and grasping with the 'pointing end' of the handle. However, by 6 years, the majority of control children planned for end-state comfort. By comparison, the proportion of end-state comfort grasps in WS children did not increase with chronological age. However, when the proportion of end state comfort grasps was plotted as a function of BPV age equivalent, a significant association was found. This may indicate that the handle task requires a cognitive ability which is indexed by BPV age, or it may indicate that children with greater BPV age were using covert verbal strategies to help them. In addition, a sub-group of children with WS showed a pattern of performance that was not seen in even the youngest typically developing children. These WS children tended to reach with the thumb up on every trial, and importantly, children who showed this stereotypical reaching pattern were distributed across the BPV age range. Lastly, a group of children with WS scored as well as typically developing children of the same age. This ability, then, to plan ahead in simple actions, seems to be unevenly distributed in children with WS. Further work will need to be done to identify whether differences between individuals with WS on tests like there are correlated with the extent of the deletion in the WS critical region, or are related to different compensatory strategies that WS children have learned, or have developed for themselves.

8.3 FURTHER RESEARCH

These studies raise a number of questions which could be addressed by further research. One question that arises from the selection for action literature, is whether there are limits on which objects are processed as potential reaching targets. For instance, are distant objects or objects which are not generally manipulated, nevertheless processed by selection for action mechanisms? This question could be addressed by presenting infants with objects of increasing size and observing at what point infants stop making reaching responses. A related question is whether, when presented with objects which are too large to grasp even with both hands, infants reach for the edges of such objects. Such studies would provide important information about how the visual world is parsed according to action potentialities.

One problem of this research was to find a method of testing looking responses to the graspability of objects that is independent of the visual salience of the objects presented. It would be possible to balance the visual salience of graspable and ungraspable objects, by using objects which are visually similar, but either afford or do not afford grasping, such as discs with or without a graspable rim. Again, the effects of side biases in reaching could be diminished if infants were presented with a vertically oriented object at the midline which was designed to have a 'graspable end' and an 'ungraspable' end. (Professor Rachel Clifton, personal communication).

It would also be interesting to attempt to replicate the result from experiment 3 but with objects that are within reach or out of reach. If it could be shown that infants are more likely to reach for an out-of-reach object when it is made more visually salient, this would provide support for the hypothesis that looking preferences can affect how infants' knowledge about is demonstrated using reaching measures.

Again, the studies on children with Williams syndrome have raised a number of questions that could be addressed by further research. Longitudinal studies would provide stronger evidence for an atypical developmental in the control of prehension. There also is some indication in the WS data of a relationship between the accuracy of grip scaling and perceptual size matching. As typically developing children between 5 and 6 show a wide range of scores on the size matching task, it would be interesting to compare grip scaling and size matching in a larger sample of 5-6 year olds, to test whether there is a relationship between these two measures in early childhood. Results from this study would provide evidence on the how far ventral and dorsal streams are independent in early childhood. It would also be useful to try to determine exactly where the strengths of WS children in object and face recognition lie, by using a range of recognition tests with objects and faces, varying the extent to which objects or faces differ along a single dimension, and the number of features by which one object differs from another.

Another important question is what determines whether an individual with WS scores well or poorly on motor planning tasks. One possibility is that performance is related to the ability to perform mental rotation. This could be tested by giving children mental rotation tasks, comparing the ability to mentally rotate images with the ability to mentally rotate body parts. Given the correlation between scores on this task and a measure of verbal mental age, it would also be useful to explicitly test whether verbal strategies are used to aid performance in WS. Lastly, it would be interesting to try movement planning tasks using everyday objects to test whether children with Williams syndrome perform better in tasks which are embedded in a familiar context.

9 References

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